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The Turbellaria of Two Granite Outcrops in Georgia

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This is a study on the Turbellaria of a specialized habitat in southeastern United States, an area which is still incompletely known as regards that segment of its fauna. Previous investigations of the biota of the granite outcrops of the Piedmont Plateau have been principally botanical. Keever, Oosting, and Anderson (1951), and others, have investigated the ecology of the plant communities; also, plant surveys and life history studies have provided the bases for a series of Master's theses at Emory University, Atlanta, Georgia. This paper presents descriptions of a new species of each of the flatworm genera *Phagocata, Mesostoma,* and *Geocentrophora,* and also some observations on their biology.

METHODS

Although the Turbellaria of the granite outcrops were observed by the writer each year from 1947 until 1951, most of the material presented here resulted from monthly collections and field observations made during the period from October 1951 to November 1952. Field work was carried out during the last two or three days of each month. Water temperatures and pH readings were taken on each collecting trip. Also, during each of the months, January, February, March, and April, the range of water temperature during a twenty-four hour period was checked with a maximum-minimum thermometer. A Hellige colorimetric kit was used for pH determinations in the field. On three occasions the dissolved oxygen in the water was measured by a micro-Winkler method.

Live specimens were brought into the laboratory for observation, especially of their reproductive and feeding behavior. Anatomical descriptions were based on whole mounts and serially sectioned specimens, the latter being used almost exclusively for definitive study of the internal anatomy. The usual fixing fluids (Bouin's, Helly's, Allen's, Gilson's, Beauchamps's) and stains (Harris' hematoxylin, Heiden-

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hains's hematoxylin, Mallory's triple) were used. A modification of the method described by Kenk (1932) was used in photographing living worms.

Acknowledgment.—The writer takes pleasure in acknowledging the help of Dr. E. Ruffin Jones, Jr., under whose direction the work was carried out, and the kindness of Dr. Libbie H. Hyman of the American Museum of Natural History, and Dr. Fenner A. Chace, Jr., of the United States National Museum in making available certain paratype material.

Fig. 1.—Southern slope of Stone Mountain.

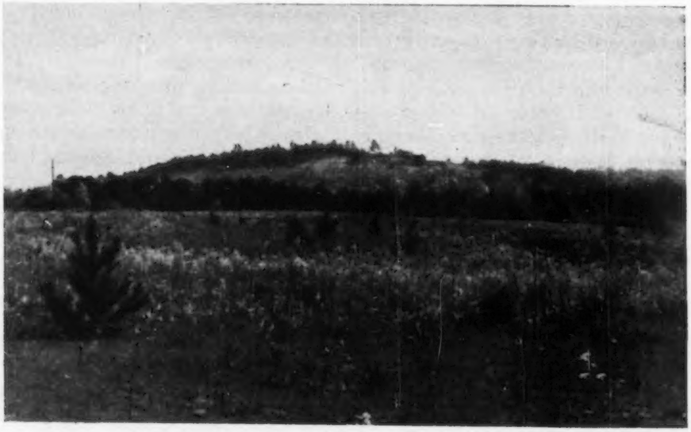


Fig. 2.—Northwestern slope of Mount Panola.

HABITATS

The localities in which the described Turbellaria occur are two granite outcrops near Atlanta, Georgia. The first, Stone Mountain (Fig. 1), located in DeKalb County ten miles east of Atlanta, is a famous scenic attraction in the area. It is a massive, dome-shaped monadnock rising approximately 1700′ above sea level and measuring 686′ from base to summit. The second locality, Mount Panola (Fig. 2), is a little-known granite outcrop twelve miles southeast of Atlanta in Rockdale County. Its summit is approximately 300′ above the base and some 1300′ above sea level.

Fig. 3.—Path of a runoff rivulet on Mount Panola showing the step-like arrangement of pools. A man's cap is shown for size relationship.

The summit and steeper slopes of Stone Mountain are exposed granite supporting principally lichens and mosses; its more gentle western slope supports patches of higher type vegetation especially in the depressions. The summit of Mount Panola, in contrast, has a cap of soil with extensive vegetation; its slopes, however, are also exposed granite. Although the runoff of rainwater over the bare rock is rapid, pools and rivulets do form in depressions and along fissures (Figs. 3, 4). There are no known springs on the outcrops, and thus the patches of vegetation which delay the runoff are important in extending the existence of the temporary pools. The Turbellaria occur in these pools and runoff rivulets. During the summer months the pools are evanescent. Between rains the exposed substrate, either bare granite or a thin layer of detritus, becomes severely desiccated and very warm. However, with the increased precipitation and lower temperatures of late autumn the pools persist for long periods. Certain of the deeper pools in more favorable locations with respect to exposure and drainage were observed to be extant from November through the first part of the following April. In the woodlands surrounding the bases of the outcrops, pools fed by the runoff have a longer seasonal duration, and following heavy rains, may exist for several days even in the summer.

The pools of the granite slopes under the most favorable conditions are seldom more than a half-meter in diameter and ten centi-

meters in depth. The water is of low mineral content and usually has a pH between 5.5 and 6.0. The extremes recorded were 5.3 and 6.8. The water temperature is greatly affected by weather conditions due to the nature of the substrate and the exposed position of the pools. During periods when the Turbellaria were present, diurnal water temperatures generally ranged between 9°C. and 20°C. During the winter, freezing and near-freezing air temperatures are common; the pools occasionally contain ice. The greatest range of water temperature recorded for a twenty-four-hour period was 0°C to 18°C. On two occasions the dissolved oxygen content of the water measured 8.8 ppm and on a third occasion 11.2 ppm.

The plants in the pools are principally filamentous algae. The algae occur most commonly along the moss-edged patches of vegetation where water seeps out into the rivulets and pools. The macrofauna, exclusive of the Turbellaria, consists of representatives of the following groups: Amphipoda, Collembola, Corixidae, Dytiscidae, Hydrophilidae, Tipulidae, and Tendipedidae. Collembola far exceed other groups in numbers of individuals present. The more nearly permanent pools at the base of Stone Mountain had large numbers of the isopod *Lirceus lineatus* Say.

ACCOUNTS OF SPECIES

Order: Rhabdocoela — Section: Typhloplanoida
Suborder: Lecithophora — Family: Typhloplanidae
Genus: *Mesostoma* Ehrenberg 1835

Mesostoma georgianum, new species
(Figs. 5, 7, 8, 9, 10, 11, 12)

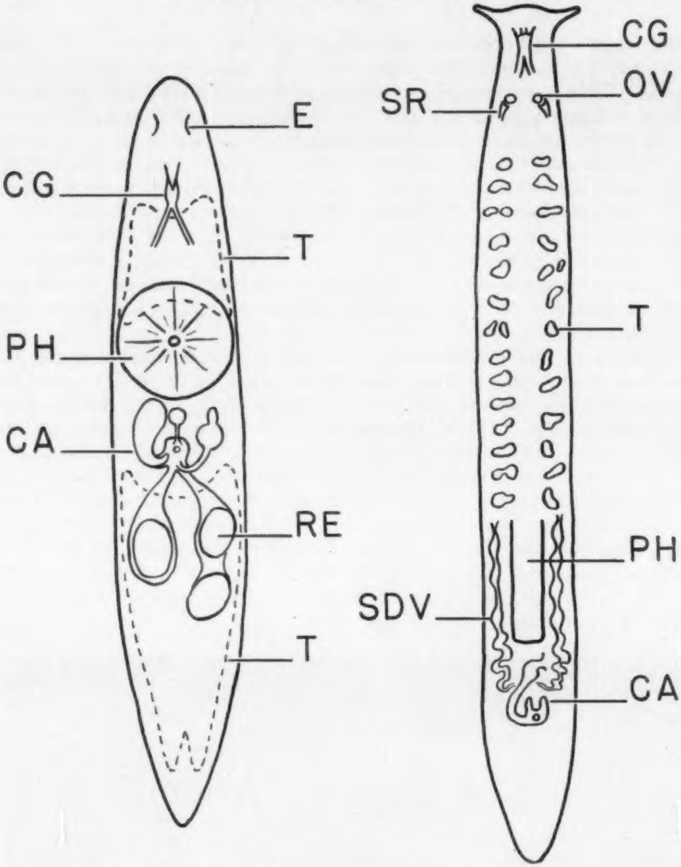
External morphology. — Sexually mature specimens, when alive, are 4-6 mm in length. The body is cigar-shaped, rounded anteriorly and tapered posteriorly. In a transverse plane the body is round; however, in the posterior half an elongate groove midway between the dorsal and ventral surfaces is present in the lateral body wall. The black pigmentation is so dense that it prevents the observation of internal structures in the living worm or in a whole mount preparation. Patches of less dense pigmentation on the lateral head surfaces indicate the position of sensory areas. On the ventral surface the genital pore is midway between the anterior and posterior ends. The mouth lies just anterior to the genital pore.

Epidermis. — The epidermis is a single layer of uninucleate, pavement-like cells with an average height of 7μ. There is no consistent difference between the measurements of the dorsal and ventral layers. The surface dimensions of these cells vary greatly. Most frequently the width is between 40μ and 60μ, but adjacent cells may have extremes as great as 175μ and 25μ. The nuclei of the epidermal cells are polymorphic, thus being in conformity with Luther's findings (1904:5) on many other species of *Mesostoma*. Ferguson and Hayes (1941) attributed this type of nucleus to the epidermal cells of embry-

onic worms only. Such is not the case in *M. georgianum,* for polymorphic nuclei were seen consistently in mature as well as young forms. This species, along with *M. macroprostatum* Hyman, is unusual in that the pigment is contained within the epidermal cells as well as in the mesenchyme. Pigment granules lie in the distal third of the epidermal cells. Other darkly pigmented species, *Mesostoma virginianum* Kepner, *et al., M. torgarmensis* Ruebush, *M. baoensis* Ruebush, have only mesenchymal pigment. Hyman (1939a) called attention to the peculiarity of pigment distribution in *M. macroprostatum;* for in that species it is denser ventrally than dorsally. Such a variation in distribution was noticed in *M. georgianum* only in the mouthpore region; in other parts of the body, dorsal and ventral pigmentation are about equal.

Rhabdites are not present. Rhammites, on the other hand, are distributed over the entire body surface and, except for the head region, are less numerous on the ventral surface of the body. Four rhammite tracts ("Stäbchenstrassen") converge and open on the anteroventral surface of the head. These tracts, two dorsolateral and two ventrolateral to the brain, are supplied by four clusters of rhammite-forming cells lying just anterior to the pharynx. Over the remainder of the body small packets of rhammites are present inside the integumentary muscle layers. Extruded rhammites in sectioned material measured 20μ to 25μ in length. A basal membrane underlies the epidermis. Cilia, 7μ-8μ long, are evenly distributed over the entire body surface.

Fig. 4.—A dried rivulet and pool bed on Mount Panola. Under favorable conditions of moisture the rivulet, seen here as a dark streak leading to the pool bed at left center, was one of the few habitats in which specimens of *Geocentrophora marcusi* were found consistently.



Figs. 5, 6.—Outline of the internal anatomy. 5. (Left).—*Mesostoma georgianum*. 6. (Right).—*Phagocata bursaperforata*. The following abbreviations are used: ADL, accessory dorso-lateral nerve; AN, anterior nerve; BC, bursa canal; BG, basophilic granules; BID, bursa-intestinal duct; BS, bursa stalk; BV, bursa vesicle; CA, copulatory apparatus; CG, cerebral ganglion; CML, circular muscle layer; COD, common ovovitelline duct; CP, ciliated pit; DL, dorso-lateral nerve; DN, dorsal nerve; DP, dorsal atrial pocket; E, eye; EB, ejaculatory bulb; ED, ejaculatory duct; EG, eosinophilic granules; FA, female antrum; FC, female canal; GA, genital atrium; GIC, genito-intestinal canal; GP, genital pore; GV, germovitellarium; MA, male antrum; OD, oviduct; OV, ovary; PB, penis bulb; PG, prostatic gland cell; PH, pharynx; PN, posterior nerve; PP, penis papilla; PS, penis stylet; PV, penis valve; RE, resistant egg; RPI, right posterior intestinal trunk; SBC, stalk of the bursa canal; SD, sperm duct; SDV, spermiducal vesicle; SG, shell glands; SPH, sphincter; SR, seminal receptacle; SV, seminal vesicle; T, testis; U, uterus; VD, vitelline duct.

Muscular and excretory systems. — The body musculature consists of dorsoventral, tangential, and longitudinal muscle fibers. The last named are evident only in the anterior half of the body where they originate in the pharyngeal region and insert on the integument of the head. The subepidermal musculature, lying under the basement membrane, consists of an outer circular layer and an inner longitudinal layer. A diagonal layer, reported for several other species of *Mesostoma* (Luther, 1904) was not detected. The excretory system follows the plan typical of the genus. Paired anterior and posterior collecting tubules join lateral to the pharynx to form common collecting tubules. These pass ventrad and mesad and open into the pharyngeal cavity at an acute angle. There is no cavity or dilation set off as an excretory beaker.

Digestive system. — In fixed material the intestine extends from a point midway between the head tip and the pharynx to the posterior end. It is cylindrical and lacks diverticula. The gastrodermis does not present important differences from that of other members of the genus. It consists of the more numerous phagocytic cells, highly vacuolated, and the eosinophilic granular club cells ("Körnerkolben"). The latter type is frequently more numerous dorsal to the pharyngeal orifice than in the extremities of the intestine. A muscularis surrounding the intestine was not seen. This concurs with Luther's findings on other species (1904:53), although he mentioned that Vogt and Yung claim to have discerned such a layer in *Mesostoma ehrenbergii* (Focke). A membrane of flattened epithelium, lacking the typical gastrodermal cells but containing muscle fibers, extends posteriorly over the inner pharyngeal orifice.

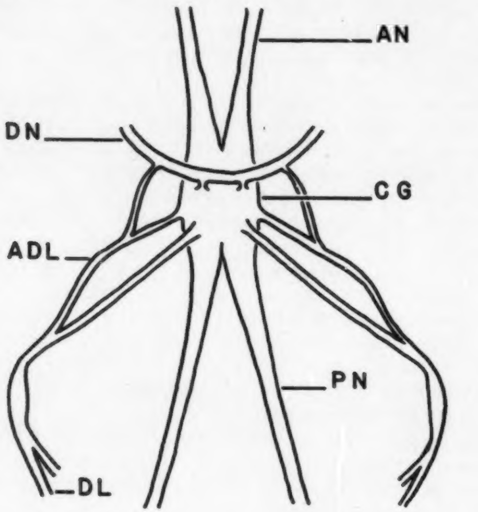
The pharynx is located slightly more than one third of the body length from the anterior end. It is the rosulate type of bulbous pharynx characteristic of the typhloplanid rhabdocoels. Since numerous specimens were available, variation in the size of the pharynges was measured to determine what degree of similarity exists in these soft-bodied animals after fixation. Only specimens having the following characteristics were used: 4-6 mm in length when alive, sexually mature, and fixed in Beauchamp's fluid. Measurements tabulated below are to the nearest 15μ since no attempt was made to estimate between the lines of the ocular micrometer.

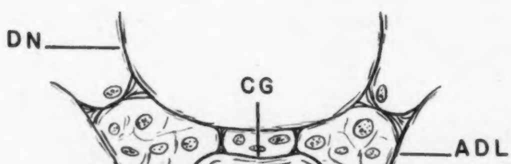
Axis	Number of Specimens	Observed Range	Mean	Standard Deviation
Transverse	14	450-585μ	515μ	36.96μ
Anteroposterior	24	450-615μ	534μ	38.69μ
Dorsoventral	24	315-420μ	359μ	23.50μ

In eleven frontally-sectioned specimens the number of longitudinal muscle fibers, lying just peripheral to the inner circular group, showed small variation: one specimen had 31 fibers, four had 34, four had 35, and two had 36. Near the distal end of the pharynx a protrusion

of the epithelium forms a circular fold, or seizing lip ("Greiflippe"), with a median groove.

Luther (1904:47) distinguished two types of pharyngeal glands, erythrophilic salivary glands and cyanophilic slime glands, the latter often lying outside of the pharynx proper. Gelei (1933) further distinguished two kinds of salivary glands, acid fuchsin staining one type red, the other rose. In *Mesostoma georgianum* three types of pharyngeal glands are present which correspond, at least in staining proper-





Figs. 7-8.—*Mesostomum georgianum*. 7.— Cerebral ganglion and related nerves, dorsal view; a reconstruction based on serial transverse sections. 8.— Transverse section through the cerebral ganglion, showing the points of origin of the dorsal nerve and the accessory dorso-lateral nerve. See Figs. 5-6 for explanation of abbreviations.

ties, to those described by Gelei. The extrinsic slime glands are blue following Mallory's triple stain, and brown following Heidenhain's hematoxylin-eosin. One type of salivary gland stains red with Mallory's, and black with Heidenhain's hematoxylin. The second type of salivary gland stains an orange-red with Mallory's stain but takes only eosin in a Heidenhain's hematoxylin-eosin preparation. All three types of glands discharge into the median groove of the seizing lip of the pharynx, the ductules of the slime glands being ventral to those of the salivary glands. The pharyngeal chamber is lined with an epithelium having two to three nuclei and a finely papillose border.

Nervous system and sense organs. — The gross morphology of the nervous system resembles that of other members of the genus. The cerebral ganglion, or brain, 80μ-110μ wide and 40μ-60μ high, lies about midway between the pharynx and the anterior end of the body (Figs. 7 and 8). Two pairs of nerve trunks extend posteriorly from the cerebral ganglion, the dorso-lateral trunks and the ventral longitudinal trunks. The latter are connected just posterior to the pharynx by a transverse commissure. A pharyngeal nerve ring is present, but its connection with the ventral longitudinal trunks could not be demonstrated.

In one feature of the nervous system *Mesostoma georgianum* differs from most other members of the genus in which the system is known. It has a single pair of anterior nerve trunks, whereas three pairs is the usual condition (Luther, 1904:67). This apparent reduction is probably a result of fusion and may be related to the anterior position of the eyes (see below).

The anterior and the ventral longitudinal trunks arise as anterior and posterior continuations of the brain. In addition to these, three pairs of smaller nerves originate from the brain, the dorsal nerve, the accessory dorso-lateral nerve, and the dorso-lateral nerve. The dorsal nerve, connected to the brain by two groups of fibers, curves dorsally around the anterior end of the intestine. Near its origin fibers leave it to join the accessory dorso-lateral nerve, which originates at the same level of the brain but from its ventro-lateral surface. The accessory dorso-lateral nerve turns posteriad and joins the root of the dorso-lateral nerve at the latter's point of flexure. After receiving the fibers of the accessory nerve, the dorso-lateral, which originates from the dorsal surface of the brain at the latter's point of bifurcation, sends a small branch ventro-posteriad, then itself continues posteriad beyond the pharynx.

The two eyes, each of which is 80μ-100μ in length and 40μ-50μ in height, are located 150μ-200μ anterior to the brain, whereas usually in members of this genus the eyes lie close to the brain, often in contact with it (Luther, 1904:78). The eyes are well separated, and there is never an anastomosis of pigment between them. The pigment is C-shaped in transverse sections. Within the cup on its lateral side is a finely striated, non-pigmented layer resembling the "Stiftchenkappe" in Luther's illustration of the eye of *Mesostoma ehrenbergii* (1904, pl.

III, fig. 25). Lateral and slightly anterior to the eyes are the sensory pits. These are faintly visible on the living worms, being more distinct in immature specimens. In sectioned material the area is invaginated and has an abundant nerve supply. The epidermal cells of these areas are normal as to size and ciliation, but contain few pigment granules. No sensory bristles were observed in the sensory pits or on other parts of the body surface.

Reproductive systems. — In fixed material the genital pore lies some 210μ to 250μ posterior to the mouth pore. Genital and mouth pores do not open into a common cavity. The common genital atrium is lined with tall, goblet-shaped epithelial cells. The five openings into the common atrium are arranged as follows: through the posterior wall open the paired uteri; immediately dorsal to these opens the common female canal; anteriorly and to the right the bursa canal opens through the dorsal wall; and the male canal enters the lower left side. Median to the opening of the male canal the dorsal atrial wall appears evaginated and forms a dorsal atrial pocket lined with typical columnar epithelium. The female portion of the reproductive system is very similar to that of *Mesostoma macroprostatum.* The finger-like ovary, its blind end directed anteriorly, merges without sharp transition into the egg-filled oviduct. The oviduct, which is 70μ-85μ in diameter, has the appearance of being pushed into the seminal receptacle. Longitudinal muscle fibers pass from the oviduct to the seminal receptacle and radiate over its outer surface. The seminal receptacle is not a temporary dilation of the female canal, but a distinct, globose structure having obvious differences from the female canal proper regardless of the amount of sperm contained in it. The diameter of the seminal receptacle ranges from 150μ when empty to 315μ when full of sperm. In addition to radiating oviducal muscle

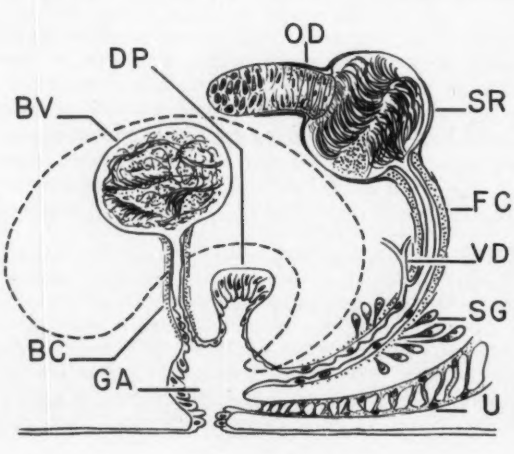


Fig. 9. — Copulatory organs of *Mesostoma georgianum,* lateral view; penis is shown in outline only. See Figs. 5-6 for explanation of abbreviations.

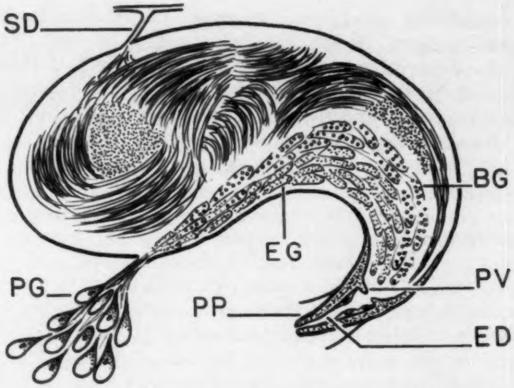


Fig. 10.—Penis of *Mesostoma georgianum*. See Figs. 5-6 for explanation of abbreviations.

fibers the wall of the seminal receptacle has an inner muscle layer and a flattened, enucleate epithelium. Distal to the seminal receptacle the female canal is lined by a smooth-surfaced epithelium with nuclei limited to the distal half of the canal. Outside the epithelium is a thick layer of circular muscle fibers. Although no sphincter is present at the proximal end of the canal, the circular muscle layer is thickest there, 15μ-17μ, and rapidly diminishes distally. Separate longitudinal muscle fibers, approximately 24 in number, form the outer layer of the canal. The common vitelline duct joins the anterior surface of the female canal just distal to the midpoint of the canal's length. At about the same level the ductules of the unicellular shell glands enter the female canal on its posterior surface.

The vesicle of the bursa copulatrix is a globose, thin-walled structure varying in diameter from 70μ when empty to 300μ when full of ejaculum. The bursa canal has a heavy inner layer of circular muscle fibers and a thin outer layer of longitudinal muscle fibers. A group of extrinsic muscle fibers, originating on the wall of the common atrium, passes dorsad to insert on the antero-ventral surface of the bursa vesicle and radiate over its outer surface. The uteri appear identical to those of *Mesostoma macroprostatum*. From the point of entrance into the common atrium, where they are joined, each extends laterad and posteriad. An anterior branch of the uterus is not present. Only hard-shelled, resistant eggs were present in the uteri; eleven was the largest number in any one animal. The mean diameter of 276 eggs, measured after deposition, was 387μ, the range 255μ to 480μ. The yolk follicles extend from the brain region to the posterior end of the body but may be absent in the region of the copulatory organs. Where the testes and yolk follicles occur at the same level in the body,

the latter are always ventral to the testes. In the middle of the body and at the extremities, where testes may not be present, the yolk follicles are dorso-lateral in position. The collecting ductules of the vitellaria could be traced only in the genital region where the two larger collecting ducts join to form the common yolk duct; the latter enters the female canal as previously described.

The penis, consisting of oval bulb and conical papilla, lies with its long axis in line with that of the body. The bulbous anterior end of the penis contacts the posterior surface of the pharynx; it varies in diameter from 120μ to 360μ depending on the amount of sperm and secretion contained. Posteriorly the bulb narrows and at the level of the genital atrium bends ventrad then anteriad, the penis papilla thus projecting anteriorly into the male atrium on the left side of the common atrium. Straight-line measurements of the penis length from its blind end to the outer curve of its flexure varied from 300μ to 500μ. The sperm ducts enter the dorsal surface of the penis bulb near its anterior end; at a slightly more posterior level the prostatic glands enter the ventral surface. The seminal vesicle occupies principally the anterior, or proximal, end of the bulb; however, the sperm mass extends in diminishing amounts to the point of flexure. The granular secretion of the prostatic glands fills the remaining ventral and distal parts of the bulbar lumen. As is typical in this genus of worms, the secretion is made up of strands of coarse, hematoxylin-staining granules and strands of finer, eosinophilic granules. The wall of the penis bulb consists of an inner, flattened epithelium, a circular muscle layer and an outer layer of longitudinal muscle. The greater bulk of the wall musculature is from the insertion fibers of five groups of heavy extrinsic muscles (Fig. 11). These fibers spread out over the penis bulb appearing in sectioned material as diagonal, circular, or longitudinal layers depending on the portion of the bulb examined. A muscular, bicuspid valve separates the penis bulb from the conical penis papilla. The lumen of the papilla is wide proximally and narrows distally forming the ejaculatory duct. It is lined with a syncitial epithelium; nuclei are present in the epithelium only in the proximal, enlarged portion of the lumen. The musculature of the papilla consists of circular fibers with a few longitudinal fibers entering from retractor muscles. The papilla, 95μ to 120μ in length, projects into

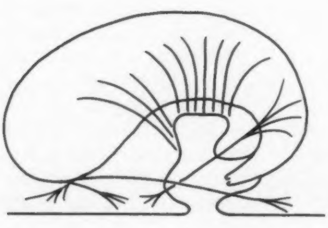


Fig. 11.—Extrinsic musculature of the penis of *Mesostoma georgianum*.

the male atrium, a cavity which, in contrast to the common genital atrium, is lined by a thin, enucleate epithelium folded into villi-like structures.

The follicular testes, dorsal in position, consist of an anterior and a posterior mass. The anterior mass extends from the cerebral region to the pharynx. Presumably it consists of right and left lobes, but the fusion is complete thus producing a single dorsal plate of follicles. The posterior mass extends from a point just behind the copulatory organs to the posterior end of the body. This mass divides into right and left lobes only at its anterior and posterior extremities. Paired anterior and posterior collecting ducts, which receive sperm ductules from the follicles, join at the level of the genital atrium to form the paired sperm ducts. These pass anteriad along the dorsal surface of the penis bulb entering it separately at an acute angle without the formation of false seminal vesicles.

Chromosomes. — The diploid chromosome number in *Mesostoma georgianum* appears to be four. The following have been reported for other species of *Mesostoma:* 4, 6, 8, 10, and 16 (Husted and Ruebush, 1940; Makino, 1951). At mitotic metaphase both pairs of chromosomes measure about 12μ in length. They are morphologically distinguishable, one pair having a median centromere, the other having a submedian centromere and a subterminal constriction on the longer arm.

Diagnosis. — Ferguson and Hayes (1941) in their synopsis of the genus *Mesostoma* cautioned against the use of highly variable characteristics in diagnoses and enumerated anatomical features which they considered as having taxonomic value. Hyman (1938, 1939a, b), Ruebush (1939), Papi (1949) and Marcus (1951), in general, used these anatomical features in diagnoses. It is therefore these features which will be emphasized in describing the taxonomic position of *Mesostoma georgianum.*

Mesostoma georgianum falls into the small group of species (*Mesostoma canum* Weiss, *M. baoensis* and *M. macroprostatum*) which are characterized by noncuticularized ejaculatory ducts and uteri lacking anterior extensions. Distinctions between *M. georgianum* and these three forms are as follows. *M. canum* lacks the conical, valve-containing penis papilla of *M. georgianum;* also, in *M. canum* the bursa canal opens into the common female canal (Weiss, 1910) rather than into the common genital atrium as in *M. georgianum. Mesostoma baoensis* lacks the type of penis papilla present in *M. georgianum,* and in addition it differs from the latter in having its genital atrium divided into inferior and superior chambers, and in the fact that its bursa copulatrix is not differentiated into vesicle and canal. *Mesostoma macroprostatum* appears to be very similar to *M. georgianum,* but the following differences exist: *M. macroprostatum* has a ventral, epidermal pit, which is lacking in *M. georgianum;* rhammite tracts, present in *M. georgianum,* are lacking in *M. macroprostatum;* in the penis bulb of *M. macroprostatum* the seminal

vesicle is separate from the prostatic vesicle, whereas no such separation exists in *M. georgianum.*

The points of difference between *M. georgianum* and *M. macroprostatum* need additional consideration; as noted by Hyman, the specimens, from which the description of the latter were made, were in poor histological condition and were reproductively spent. With regard to the absence of rhammite tracts in *M. macroprostatum,* there is no basis for believing that this was due to the senescent condition of the type material. Specimens of *M. georgianum* collected near the end of the breeding season had rhammite tracts even though they appeared senescent by other criteria. The second point of difference, the presence of an epidermal pit ("Hautblindsack") in *M. macroprostatum,* was overlooked by Hyman when she described the species. It was noticed by the writer while studying paratype slides kindly lent by Dr. Libbie H. Hyman and by the United States National Museum. Fine histological detail could not be attempted; however, the position and morphology of the structure appeared to fit the description of a "Hautblindsack" as given by Luther (1904:80- pl. I, fig. 37). The ventral, epidermal pit is not known to occur in any other *Mesostoma* species; indeed, the diagnostic characters separating it from *Bothromesostoma* are the presence in the latter of a ventral, epidermal pit and of a ductus spermaticus (Graff, 1913:263). Although the pit can be taken as further evidence of the close relationship between these two genera, a change in the taxonomic position of *M. macroprostatum* should await the study of more favorable material.

Although the penis papilla of *M. georgianum* and *M. macroprostatum* appear identical, the penis bulbs of the two are different, since there is no separation of the seminal and prostatic vesicles in *M. georgianum* as there is in *M. macroprostatum.* The relative position of the two vesicles in *M. georgianum* appears to be intermediate between the extreme condition present in *M. macroprostatum, M. artica,* and *M. macropenis* (Hyman, 1938, 1939b) and that of *M. lingua* (Luther, 1904:99, fig. 11) in which the two vesicles occupy equal halves of the penis bulb.

Differential diagnosis. — In having both a non-cuticularized ejaculatory duct and uteri lacking anterior extensions, *Mesostoma georgianum* differs from all other species of *Mesostoma* except *M. canum, M. baoensis,* and *M. macroprostatum.* It can be distinguished from these three as follows: from *M. canum* by the presence of a valve in the penis and by the fact that the bursa canal opens into the genital atrium rather than the female canal; from *M. baoensis* by the presence of a valve in the penis papilla and a bursa copulatrix differentiated into a vesicle and a canal, and in lacking superior and inferior chambers in the genital atrium; from *M. macroprostatum* by the presence of rhammite tracts and by the lack of a ventral epidermal pit and a separated prostatic and seminal vesicle.

Type material. — Approximately 110 specimens of *Mesostoma*

georgianum were prepared for microscopic study. The type material is deposited in the United States National Museum: *holotype,* whole mount, USNM 29733; one *paratype,* serial sagittal sections (two slides) USNM 29734; one *paratype,* serial transverse sections (three slides) USNM 29735. The type locality is Mt. Panola, Rockdale Co., Georgia.

Feeding habits. — Although specimens of *Mesostoma georgianum* feed on various small animals which fall into the pools, their chief prey is the collembolans which are present on the water surface in large numbers. As these insects rest on the water film, the worms, gliding under the film, contact and adhere to them with the ventral surfaces of their heads. The rhammite secretions very probably aid in this process. The worm manuevers its body under the prey, bringing its mouth pore into a position from which the protruding pharynx can contact the insect and suck out its soft parts. Of the three species of Collembola which inhabit the pools, *Isotomurus palustroides* Folsom is the most abundant and the most frequently attacked.[2] The other two species, *Sminthurus* new species and *Sminthuroides malmgreni* (Tulberg), are apparently less important as food sources; the former is captured by the worms but it is the least numerous of the collembolans, while the latter was never observed under attack by the worms.

In the laboratory *Mesostoma georgianum* was fed on beef liver, ants, tendipedid larvae and on injured amphipods, snails, leeches, damselfly nymphs and mosquito larvae. The worms were especially aggressive in attacking red midge larvae, even uninjured individuals twice their size. Having contacted and encircled the body of these larvae, the worms were not dislodged by the violent thrashings of the larvae as it attempted to escape.

Papi (1949) suggested that recently hatched specimens of *Mesostoma benazzi* Papi feed on microplankton in nature. In this connection no direct comparison between this species and *M. georgianum* can be made, since no specimens known to be of comparable age were observed by the writer. However, the smallest specimens of *M. georgianum* (1-1.5 mm) fed and matured in the laboratory on the same diet as did the larger forms.

Life cycle.— Large numbers of *Mesostoma georgianum* are present in the outcrop pools. This abundance, as well as the small size of the pools, facilitated the capture of desired specimens and observations of their life habits. They are very active and are commonly found gliding ventral side up under the surface film in direct sunlight. Neither in the field nor in the laboratory was there any indication that they avoid or are injured by continuous, direct sunlight. Although they can suspend themselves by a mucus thread in descending from the surface

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[2] Dr. Harlow B. Mills and Mr. W. R. Richards of the Illinois State Natural History Survey kindly identified the collembolans. Mr. Richards plans to publish a description of the new species of *Sminthurus.*

film to the substrate, as reported for other mesostomine worms (*Bothromesostoma evelinae* Marcus and *Mesostoma ehrenbergii* (O. Schmidt)), none, not even the smallest, was seen to swim freely in the water as does *M. productum* (Gelei, 1933).

The active phase of the life cycle of *Mesostoma georgianum* extends from October to the following April. In having its active phase in the winter rather than in the summer, it is similar to *M. benazzi,* but differs from other members of the genus whose life histories are known. From October through the winter, the young worms hatch from resistant eggs presumably deposited the previous season. None of twelve of the largest specimens collected early in November was sexually mature; however, in ten of the twelve individuals developing sex organs were recognizable. Development of the main parts of the reproductive system in an individual is almost simultaneous. Penis, testes, ovary, and bursa copulatrix are formed first, seminal receptacle and uteri shortly afterward. The genital pore was perforate only in those forms having completely formed organs. From November through April all large specimens examined were sexually mature, although small, immature specimens were also present during the same period. Copulating pairs were observed in the field during each month in which mature specimens were found.

Typically in typhloplanid worms, thin-shelled, or subitaneous, as well as thick-shelled, or dormant, eggs are produced (Hyman, 1951a:135). The former type is produced in the early part of the breeding season, usually in summer, and hatched immediately. In *Mesostoma georgianum* only the thick-shelled type egg is produced. From late November through the breeding season mature worms contain these orange eggs. The peak of egg production is reached in January and February. Twenty specimens, collected during those two months, averaged five eggs per individual. Whether these eggs can hatch in the same season after a short period of dormancy, or whether they must remain dormant until the following season was not determined. Papi (1949) reported that the eggs of *Mesostoma benazzi,* all of the thick-shelled type, would hatch only after a dormancy of at least six months. He concluded that in that species only one generation was produced in a season. It is possible that the same hatching characteristics obtain in *Mesostoma georgianum,* thus specimens found late in the breeding season may have hatched from eggs deposited the previous season.

Attempts to hatch eggs in the laboratory were unsuccessful. Both laboratory and field deposited eggs were used. The following variations, using rainwater or outcrop pool water, were employed in attempts to stimulate hatching: submersion of the eggs for five weeks at room temperature; submersion in water cooled to 15° C.; chilling the water at night only; desiccation of the eggs followed at various intervals by submersion in cool water.

Since no animals appearing reproductively spent were seen until April, it is probable that the life span of *Mesostoma georgianum* may

be four to five months. Two months was the longest that they could be maintained in the laboratory.

Copulation. — Information on copulation among the species of *Mesostoma* has been reported in only a few instances (Luther, 1904; Bresslau, 1933). Serial section studies of copulation in species of *Mesostoma* have never been reported, although Luther (1904:114) mentioned that Fuhrmann made such studies on a species of the closely related genus *Bothromesostoma. Mesostoma georgianum* was observed in copulation both in the field and in the laboratory on numerous occasions, thus there was an opportunity for the study of the internal organs by sectioned material as well as for observations on the behavior.

Bresslau (1933:159) stated that a kind of "Liebespiel" often precedes the copulatory act in Turbellaria; he mentioned in particular *Convoluta, Gyratrix, Dalyellia* and *Mesostoma.* Hyman (1951a:127) indicated that such behavior, or "courtship," occurs in many species throughout the class. Behavior of this type was frequently seen in *Mesostoma georgianum.* A pair of worms, each with its anterior end pressed into the partner's mouth-genital pore region, move in a circle, the anterior ends pushing into the partner's mid-section in a pulsating motion. This can take place with the animals adhering to the surface film, on the sides of a container, or on the substrate. The "courtship" lasts from two to four minutes and usually, although not invariably, terminates in the animals assuming a copulation position. In a few instances a third worm was observed to intrude, disrupt the "courtship" behavior, and replace one of the partners. The process was then resumed with the intruder as participant.

Concerning the copulation positions of Turbellaria in general, Hyman (1951a:127) stated, "Usually the copulants face more or less away from each other with the genital regions pressed together and often elevated, the rest of the body attached to the substratum. A parallel position, however, is not infrequent in the same species." Although *Mesostoma georgianum* copulants were often seen in the first position mentioned by Hyman, the position often changed to a parallel or to an "X" position even in the same pair. Indeed, it was the rule rather than the exception for copulants in this species to change to all three positions during the course of one copulatory act.

In eight instances the duration of the copulatory act was timed. Although many more copulating pairs were observed, it was rare that the copulants were noticed at the instant of pairing. The durations of eight timed acts were: 35, 39, 39, 40, 40, 43, 50, and 63 minutes. In comparison with other Turbellaria in which copulation has been studied this is a relatively long, but not exceptional, duration for the process. In the order Acoela the duration of copulation is known to vary greatly: one and one half minutes in *Polychoerus carmelensis* (Costello and Costello, 1938) and fifty minutes in *Amphiscolops langerhansi* (Hyman, 1937a). Kato (in Hyman 1951a:127) observed certain polyclads to remain in copulation for an hour or more. Luther

(1904:226) reported fifteen minutes as the copulation time in *Mesostoma lingua* (Abildgaard).

Six pairs of worms were fixed *in copula.* Four of these pairs remained together after fixation and throughout slide preparation. One of the separated individuals was ruined and thus eleven individuals were available for study in serial sections, sagittal and transverse. In no case was fixation effected before at least partial withdrawal of the copulatory organs had taken place. The degree of retraction varied; those showing least retraction had the copulatory organs and the atrial complex pushed to the outside though not in contact with the organs of the partner. Such specimens were assumed to most nearly represent the normal position of the organs during copulation (Fig. 12). The penis papilla as well as the distal third of the penis bulb project to the outside, and the dorsal atrial pocket comes to lie along the median surface of the papilla. The degree of eversion may be so extreme that the bursa vesicle is displaced to a position ventral to the normal level of the ventral body wall. The distal portion of the bursa canal is everted and the remaining part so contracted that the

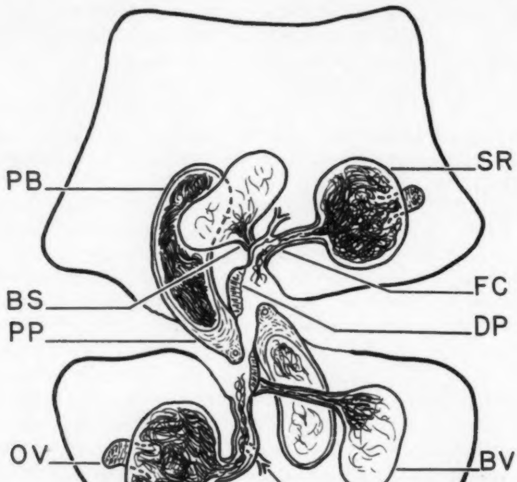


Fig. 12.—Composite drawing of reproductive organs of *Mesostoma georgianum* fixed *in copula;* based on serial transverse sections. See Figs. 5-6 for explanation of abbreviations.

canal is no more than one-sixth of its normal length. The eversion of the common atrium brings the opening of the female canal to the outside; accordingly the seminal receptacle, oviduct, and ovary are much more ventral in position than is normal.

It is thought that among Turbellaria having both bursa copulatrix and seminal vesicle, copulation is effected by the insertion of the penis of one copulant into the partner's bursa canal, the ejaculum being deposited in the vesicle of the bursa and later transferred to the seminal receptacle. Duges, Kennel, Burr and Wilhelmi are cited by Hyman (1925) as concurring in this concept. Luther (1904:114) related that Fuhrmann's account of copulation in *Bothromesostoma personatum* stated that sectioned material showed the penis to be inserted into the bursa canal of the partner. Moreover, Graff observed that in *Mesostoma ehrenbergii* the ejaculum was transferred soon after copulation from the bursa to the seminal receptacle (Luther, 1904:114).

Since none of the copulants in this study was fixed with its penis still in the receiving organ of the partner, the location of the penis during copulation cannot be supported or denied by direct evidence. However, the location of the ejaculated sperm mass does present indirect evidence regarding this, for if the bursa were the recipient of the ejaculum, the transfer to the seminal receptacle occurring later, the bursae of the copulants should contain large sperm masses and the seminal receptacles little if any (it is possible that some sperm might be present in the seminal receptacle from a previous copulation). In the sectioned material examined, large sperm masses were present in the seminal receptacles of all eleven specimens but in the bursae of only six of the eleven. This disposition of the sperm mass suggests that the penis may be inserted into the female canal and the sperm deposited there as well as in the bursa copulatrix. This is further substantiated by the fact that in five of the eleven specimens large sperm masses were present also in the female canal, whereas similar masses were not present in the bursa canals.

Five worms were killed at intervals following copulation in the hope that they might aid in interpreting the conditions seen in the copulating forms. These individuals were observed during copulation until they showed sign of separating. Each pair was then removed and placed in a separate container. One pair was killed thirty minutes after copulating, another pair one day after copulating, and one individual two days after copulating. Serial sections of these worms showed that the seminal receptacles contained large amounts of sperm, the female canals contained few or none, and the bursa vesicles contained few. This likewise tends to support the idea that the seminal receptacles may receive the ejaculum during copulation; it is not conclusive, however, since the transfer of sperm from the bursae to the seminal receptacles could have taken place within thirty minutes after copulation. These observations suggest that in *Mesostoma georgianum* the seminal receptacle as well as the bursa copulatrix may receive the

sperm mass during copulation. It is not suggested that the bursa has no role as a reservoir for sperm, for many non-copulating specimens were found with bursae distended by large amounts of sperm.

Order: Tricladida Section: Paludicola
Suborder: Haploneura Family: Planaridae
Genus: *Phagocata* Leidy 1847

Phagocata bursaperforata, new species
(Figs. 6, 13, 14, 15)

External morphology. — When gliding, sexually mature specimens are 10-14 mm in length and 1 mm in width. The head is truncate; the forward margin is slightly convex. Slender, elongate auricles project antero-laterally at the angles of the head. Although the body width is nearly constant throughout most of its length, a constriction, or "neck," is present behind the auricles. Posterior to the copulatory organs the lateral body margins converge rather abruptly, forming a pointed posterior end. In large specimens the root of the pharynx is at the beginning of the posterior third of the body; in smaller specimens (less than 10 mm) it is slightly more anterior. Eyes are absent, and body pigment is entirely lacking; thus, the color, except for ingested material, is milk-white.

Epidermis and musculature. — The epidermal cells of the dorsal surface are taller (7μ-8μ) than those of the ventral surface (5μ). The cells of both layers contain epidermal rhabdites 2μ-3μ long and adenal rhabdites 7μ-8μ long, but the adenal rhabdites are more numerous in the dorsal layer. Cilia, 8μ in length, are borne only on the ventral surface median to the marginal adhesive zone. Cyanophilic slime glands lie near the ventral body wall in the anterior half of the body; these open on the ventral surface, anterior to the brain. Outlets of eosinophilic glands, whose cells lie also in the head region, are distributed in a V-shaped pattern; the apex of the pattern is directed anteriorly. The musculature of the body wall consists of two layers of fibers, a thin circular layer adjacent to the basement membrane and an inner, thicker layer of longitudinal fibers. A layer of diagonal fibers could not be demonstrated. Isolated bundles of muscle fibers, principally dorso-ventral, are scattered through the mesenchyme.

Digestive and nervous systems. — The anterior branch of the intestine has 15 to 17 pairs of diverticula, which were never observed to be anastomosed. The two posterior intestinal trunks merge at their extremities. The pharynx is approximately one-seventh of the body length. Its outer epithelium is ciliated and is apparently of the insunken ("eingesenkt") type. The outer muscular zone consists of longitudinal fibers beneath which is a layer of circular fibers of equal thickness. The epithelium of the pharyngeal lumen is not of the insunken type. The inner muscular zone consists of a thick inner layer of circular fibers and an outer layer of single longitudinal fibers. No

detailed study of the nervous system was made. The gross morphology of the system is similar to that reported for other paludicolous triclads.

Reproductive system. — The testicular follicles, 14 to 16 pairs, lie between the stems of the intestinal diverticula. None is posterior to the root of the pharynx. Internally individual follicles extend from the dorsal to the ventral body wall. Lateral to the pharynx the sperm ducts widen into sperm-filled, sinuous tubes, the spermiducal vesicles. At the level of the penis these narrow, turn dorso-mesad, penetrate the penis bulb, and join to form the ejaculatory duct. This duct traverses the length of the penis without the formation of bulbar

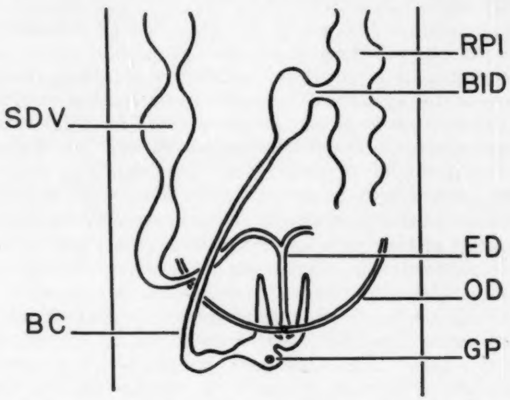


Fig. 13.—Outline drawing of the genital organs of *Phagocata bursaperforata*, dorsal view. See Figs. 5-6 for explanation of abbreviations.

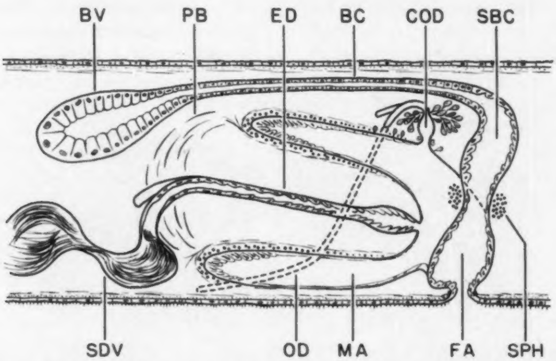


Fig. 14.—Copulatory organs of *Phagocata bursaperforata*, sagittal section. See Figs. 5-6 for explanation of abbreviations.

cavities or seminal vesicles. Its only modification is a slight dilation at the distal end of the penis papilla. The penis consists of a weakly developed bulb and a papilla about twice as long as it is wide. The papilla is cylindrical, tapering only slightly at its distal end. Near the base of the papilla the surface membranes of the columnar epithelial cells are irregular, often papillose. Distally on the papilla this epithelium becomes cuboidal and smooth. The musculature of the papilla wall consists of an outer layer and an inner longitudinal layer; the latter is much thicker in the proximal than in the distal part of the organ. Loosely organized mesenchymal tissue, lacking glandular elements, fills the body of the penis between the outer musculature and the wall of the ejaculatory duct.

The male antrum is separate from the female antrum. The epithelium of the male antrum is papillose along the roof and near the base of the penis papilla but smooth and flattened along the floor. The musculature of the antral wall is made up of a circular layer adjacent to the epithelium and an outer longitudinal layer. Posteriorly, the male antrum ends blindly; it communicates with the female antrum by an opening in the left posterior wall. The resulting common antrum is small and leads directly to the outside by the genital pore.

The female antrum, which is often expanded laterally, and the vertical portion of the bursa canal are displaced to the left. A thick, muscular sphincter terminates the female antrum dorsally and marks the beginning of the bursa canal. Dorsal to the sphincter the bursa canal is expanded; however, after turning anteriad, it narrows to a diameter of about 25μ. As it moves anteriad, it angles towards the midline of the body. The bursa vesicle, into which it opens without sharp transition, is located medially in relation to the lateral body margins. The vesicle is oval in shape and has a diameter between 70μ and 100μ. At its right anterior extremity it communicates with the right posterior intestinal trunk by a bursa-intestinal duct. This structure is not known to be present in any other species of *Phagocata;* however, it is present in certain species of other genera of the Planaridae — *Dugesia, Curtisia,* and *Rhodax*. The epithelium of the

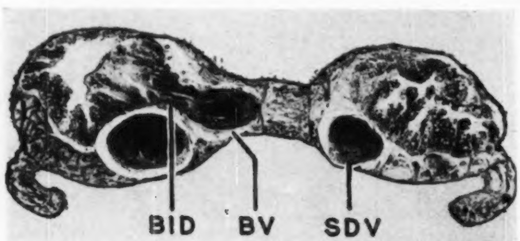


Fig. 15—Photomicrograph of *Phagocata bursaperforata,* transverse section through the bursa vesicle and bursa-intestinal duct. Sperm are present in the vesicle, bursa-intestinal duct, and spermiducal vesicles.

vertical portion of the bursa canal, as well as that of the female antrum, is a tall, papillose, columnar type, while that of the narrow part of the canal is a smooth, cuboidal type. The lumen of the small bursa vesicle is almost occluded by its relatively tall, 25μ-35μ, columnar epithelium. The entire bursa complex, canal and vesicle, is surrounded by an outer longitudinal and an inner circular muscle layer.

The paired ovaries lie on either side of the cephalic end of the anterior intestinal ramus. Seminal receptacles on the lateral surfaces of the ovaries lead into ovovitelline ducts. As they pass posteriorly, these ducts, lying just dorsal to the nerve trunks, receive minute tubules from the vitellaria. At the level of the penis the ovovitelline ducts turn dorso-mesad and merge dorsal to the male antrum forming a common ovovitelline duct. The latter receives processes from surrounding eosinophilic gland cells. A sphincter surrounds the common ovovitelline duct at the point where it opens through the roof of the male antrum. The point of entrance of the common ovovitelline duct is about three-fourths of the length of the male antrum from its anterior end.

Taxonomic diagnosis.—The arrangement of the inner pharyngeal musculature (distinct circular and longitudinal layers) in *Phagocata bursaperforata* is of the type described for the families Planaridae and Kenkiidae rather than the Dendrocoelidae (Kenk, 1930a, 1930b; Hyman 1937b). In spite of several features held in common with genera of the Kenkiidae, it lacks anterior adhesive organs and large marginal rhabdites, diagnostic characters of that family; consequently, it must be assigned to the family Planaridae.

The course of the ovovitelline ducts, their fusion, and their point of entrance into the genital atria have been emphasized as valuable generic criteria by Meixner (1928) and Kenk (1930a, 1930b). In the species described here the ovovitelline ducts, without embracing the bursa stalk, join forming a common duct which opens through the roof of the male atrium. Such an anatomical feature is present in the following genera of the Planaridae: *Phagocata, Planaria, Crenobia,* and *Polycelis.* This new form fits most closely the definition of *Phagocata* as defined by Kenk (1944), Hyman (1937c, 1951b) and Dahm (1949); for it lacks the adenodactyls characteristic of *Planaria,* the radial muscular plates characteristic of *Crenobia,* and the numerous marginal eyes characteristic of *Polycelis.* In possessing elongate auricles *Phagocata bursaperforata* does not conform strictly to the definitions of the genus as given by Hyman (1951b) and Dahm (1949). However, Beauchamp (1939) has pointed out that a small group of European *Phagocata* have similar auricles.

The natural affinities of *Phagocata bursaperforata* within the genus are difficult to discern. The external morphology and internal anatomy seem to indicate divergent relationships, a paradox which Hyman (1937c) encountered in working with certain other *Phagocata* species. In Europe the genus *Phagocata* is made up of approximately fourteen

known species and subspecies. For the most part they are slender, non-pigmented worms having small, close-set eyes and short or non-protruding auricles. Although not strict troglodytes, they are associated with underground water systems. Beauchamp (1932, 1939) has provided the most comprehensive treatment of the group.

The four Asiatic species of *Phagocata, P. papillifera* Ijima and Kaburaki, *P. vivida* Ijima and Kaburaki (Ijima and Kaburaki 1916), *P. uenoi* Okugawa, and *P. miyadii* Okugawa (Okugawa 1939), are pigmented and have eyes and short auricles. None is hypogean, although *P. papillifera* is known to inhabit wells. Of the eight North American species and subspecies all lack prominent auricles, five are pigmented, all have eyes, and only one, *P. subterranea,* is hypogean (Hyman, 1937b). Hyman has reviewed the American species (Hyman, 1937c, 1951b).

On the basis of characteristics other than those of the copulatory apparatus, *Phagocata bursaperforata* shows singularly close resemblance to the four European species: *Phagocata opisthogona* (Kenk, 1936), *P. prosorchis* (Kenk, 1937), *P. Racovitzai* (Beauchamp, 1929), and *P. notadena* (Beauchamp, 1937). Both Kenk and Beauchamp recognized these four species as forming a natural group within the genus. Indeed, Beauchamp (1939) considered them along with a *Phagocata* sp., collected in Sardinia by Benazzi, as constituting the subgenus *Atrioplanaria.* Members of this subgenus have in common the following characteristics: absence of body pigment, prepharyngeal testes, and a posteriorly situated pharynx. *Phagocata bursaperforata* is the only American species having this combination of characters. On this basis an affinity is indicated. Such characters, however, are considered to be of less value taxonomically than those of the copulatory apparatus. A comparison of the male copulatory organs of the Georgia triclad with those occurring in the European subgroup not only does not strengthen this indicated relationship, but rather vitiates it. Members of the *Atrioplanaria* group have bulbar cavities and modified male atria, structures entirely lacking in *Phagocata bursaperforata.* The male copulatory apparatus of *P. bursaperforata* does, on the other hand, show fundamental similarities with those of the American species, *P. vernalis* Kenk and *P. morgani* (Stevens and Boring). Consequently, it is suggested here that it is with these two American species that *Phagocata bursaperforata* has its closest natural affinities.

Differential diagnosis.—Phagocata bursaperforata differs from all other known members of the genus in having a bursa-intestinal duct. Also, it can be distinguished from all other known North American species of *Phagocata* by the following combination of characters: elongate auricles, prepharyngeal testes, and the absence of eyes.

Type material.—Twenty-eight sexually mature specimens of *Phagocata bursaperforata* were studied, five whole mounts and twenty-three sectioned transversely or sagittally. The type material is deposited in the United States National Museum: *holotype,* whole

mount, USNM 29739; one *paratype* (six slides) serial transverse sections, USNM 29741; one *paratype* (four sides) serial sagittal sections, USNM 29740. The type locality is Stone Mountain, DeKalb Co., Georgia.

Observations on living worms.—Specimens of *Phagocata bursaperforata* were collected at Stone Mountain and Mount Panola during every month from September until the following June. Only those taken in September and October lacked reproductive organs. Although sometimes found well up on the granite slopes of the outcrops, they were more numerous in the pools formed by the runoff at the bases.

Two to three weeks was the limit of their survival when kept in the laboratory at room temperature. At cooler temperatures, 15°C.-17°C., survival time was extended to more than three and one-half months. Copulation was never observed and cocoons never deposited even though sexually mature individuals were maintained together in the laboratory for several months. Several sectioned specimens had sperm in the common ovovitelline duct and in the bursa copulatrix; however, there was no evidence of a spermatophore as has been reported in some other species of this genus (Hyman, 1937c).

In nature they were observed feeding only on dead animals which had fallen into the pools. In the laboratory they fed on injured amphipods and injured insect larvae. On a few occasions they were seen to attack and subdue uninjured midge larvae. Although extensive experiments were not attempted, limited regenerative powers were demonstrated by severing two specimens—the first approximately one millimeter behind the "neck," the second, midway between the head and the pharynx. The severed segments of each worm regenerated the missing part. There was, however, no direct evidence that this triclad reproduces in nature by transverse fission or fragmentation.

Order: Alloeocoela
Suborder: Lecithoepitheliata
Family: Prorhynchidae
Genus: *Geocentrophora* de Man 1876

Geocentrophora marcusi, new species
(Figs. 16, 17, 18, 19)

External morphology.—When gliding undisturbed, sexually mature specimens are 3 mm to 4 mm in length. The forward margin of the head is convex with a median depression, the mouth pore. Laterally, the head is extended into prominent, pointed auricles. Posterior to the head the body margins are parallel, ending in a truncate posterior tip. The cylindrical pharynx is about one-eighth of the body length and one-half of the body width. The crescent-shaped brain overlies the anterior end of the pharynx. Two bright red eyes, the width of the pharynx apart, lie just posterior to the brain. Red pigment occurs

also in the tissue of the pharyngeal region; however, the amount and distribution of the pigment is variable. Usually it is in the form of an irregular network surrounding the pharynx. In the more heavily pigmented specimens the network may extend posteriorly two-thirds of the body length as well as anteriorly to the forward head margin, in the latter case appearing in discrete strands.

Epidermis.—The ventral epidermis consists of cells without nuclei, 3μ in height and approximately 15μ in length. Cilia, 4μ to 5μ long, are present on the ventral epidermis only. The dorsal epidermis, slightly thinner than the ventral layer, is anucleate, acellular, and finely striated. A row of fine, hematoxylin-staining granules occurs under the outer membrane of both epidermal layers.

Fine-grained eosinophilic glands and coarse-grained hematoxylin-staining glands are present. Both have their unicellular bodies lying internal to the integumentary muscle layers; their sinuous ductules penetrate the epidermis. The eosinophilic glands are restricted to the dorsal surface except for the posterior end where they are clustered on the ventral surface forming what is probably a holdfast organ. Throughout the length of the body the hematoxylin-staining glands occur beneath the ventral and dorsal surfaces, being more numerous on the latter. Deeply-staining cyanophilic cells occur in the mesenchyme; these are probably identical with the "mesenchyme glands" described by Steinböck in related species.

Muscular and excretory systems.—The musculature of the body wall consists of a compact, outer layer of circular fibers and an inner layer of separate, longitudinal fibers. Oblique and dorso-ventral bundles of muscle fibers are present in the mesenchyme; the latter are segmentally arranged between the intestinal diverticula in the posterior part of the body.

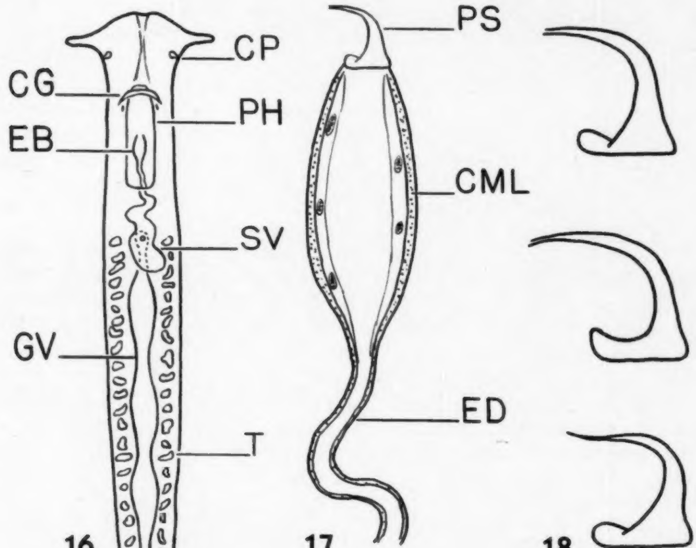
The excretory system has the basic plan found in other members of the genus. On either side of the body anterior and posterior collecting tubules join, forming two common collecting tubules. These, somewhat coiled, pass ventrad and open lateral to and at the same antero-posterior level as the female genital pore.

Digestive system.—The cylindrical pharynx has a tapered anterior end and in preserved material has the following range of measurements: length, 200μ-300μ; diameter, 100μ-150μ. The mouth canal is from one-half to one-third of the length of the pharynx and lacks cilia. The anterior tip of the pharynx extends freely into the mouth canal forming a short seizing lip. The pharynx is of the type designated as *pharynx variabilis intextus,* having the following arrangement of layers from the lumen outwards: flattened, enucleate epithelium, longitudinal muscle, circular muscle, radial muscle, circular muscle, and longitudinal muscle. This arrangement of layers is constant throughout the pharynx, and there is no concentration of circular muscle fibers in the form of a sphincter as described for *Geocentrophora sphyrocephala* de Man (Steinböck, 1927:562). Nuclei, lying

between the radial muscle sheets, are restricted to the outer half of the pharyngeal wall.

Dorsal to the root of the pharynx, the intestinal wall is evaginated anteriorly forming a dorsal intestinal pocket approximately one-fourth of the length of the pharynx; a ventral intestinal pocket is not present. The ductules of gland cells which lie near the root of the pharynx penetrate the wall of the esophagus. The intestine extends to the posterior end of the body and gives rise to twenty to twenty-five pairs of diverticula. The epithelium of the intestine consists of the typical phagocytic and glandular cells; the latter, although more numerous in the walls of the diverticula, also occur in the floor of the intestine.

Nervous system.—The crescent-shaped brain lies dorsal to the anterior end of the pharynx. It consists of paired ganglia connected by a broad commissure. Lateral to the pharynx conspicuous nerve trunks, the posterior ventral nerves, leave the cerebral ganglia, pass obliquely ventrad and extend into the posterior part of the body. These nerves lie adjacent to the subepidermal musculature of the ventral



Figs. 16-18.—*Geocentrophora marcusi.* 16.—Outline of the internal anatomy. 17.—Male copulatory organ. 18.—Variation in the morphology of the penis stylet; the uppermost shape was observed most frequently. See Figs. 5-6 for explanation of abbreviations.

body wall. Anteriorly, the brain gives rise to a pair of dorsal and a pair of ventral anterior nerves.

Posterior to the auricles paired ciliated pits open ventro-laterally. They are flask-shaped, 20μ to 30μ in length, and contain six nuclei in the epithelium of the canal. Cilia, twice as long as those of the epidermis, project from the openings of the pits. The eyes, bright red in the living worm, are 9μ in diameter. They are cup-shaped and lie the width of the pharynx apart. They are in contact with the dorsal surface of the cerebral ganglia posterior to the level of the commissure. Sensory bristles in the epidermis are apparently lacking.

Reproductive system.—The testicular follicles, arranged laterally in two rows, extend anteriorly from the tail region approximately three-fifths of the body length. Although the follicles are not strictly paired, the numerical differences between the two rows in an individual was not observed to be greater than two. In fourteen specimens the numbers of pairs of follicles ranged from fourteen to twenty-four. Of the fourteen, twelve had at least nineteen pairs of follicles.

The seminal vesicle is a sinuous tube 50μ-115μ in diameter and 300μ-375μ in length. It extends from the level of the most anterior pair of testicular follicles almost to the root of the pharynx. The point of entrance of the sperm ducts could not be determined. The posterior end of the vesicle is bulb-like; anteriorly, it narrows and leads into the sinuous ejaculatory duct. Ventral to the proximal part of the pharynx this duct widens into the ejaculatory bulb. In fixed material the bulb, lying about midway between the extremities of the pharynx, is 30μ to 50μ in diameter and 75μ to 150μ in length. The hook-shaped stylet is based at the anterior end of the ejaculatory bulb. The canal of the penis stylet opens into the mouth canal, about one-third of the distance from the end of the pharynx to the mouth pore.

The musculature of the male canal is principally a layer of circular fibers. In the wall of the seminal vesicle this layer is thin; it increases in thickness along the ejaculatory bulb. Longitudinal muscle fibers, presumably protractors, originate at the forward head margin and insert on the outside of the ejaculatory bulb. The lining of the bulb is a syncitial epithelium containing five to seven nuclei.

The penis consists of a deeply staining basal portion and a cuticular stylet surrounded by a membranous sheath. The left margin of the penis base has an anteriorly projecting protuberance containing four nuclei. The proximal part of the stylet is attached to the right side of the penis base. The shaft of the stylet forms a shallow arc to the left, the tip of the stylet thus lying in a plane almost 90° to that of the proximal part of the shaft. A membranous sheath containing approximately ten longitudinal muscle fibers surrounds the stylet. Measurements of the penis have the following ranges: width of the penis base, 20μ-40μ; length of the penis, 34μ-58μ. The distal end of the stylet is usually straight but may be slightly curved anteriorly or posteriorly. Variations in morphology of the penis stylet are shown in Figure 18.

The female system consists principally of an elongate germo-

vitellarium which extends anteriorly from the tail region for almost two thirds of the body length. At its anterior end it narrows abruptly into a short oviduct, approximately 30μ long, which leads into the female antrum. The latter opens externally through the midventral female genital pore. The shape and dimensions of the female antrum are affected by contact with the larger, dorsal-lying seminal vesicle. If not distorted by contact with this vesicle, the antrum is globose and measures 30μ in diameter. If distorted by contact with the seminal vesicle, a flattened, cone-shaped cavity results, having a height of 15μ and a width of 40μ. The female antrum is lined with a nucleated, cuboidal epithelium surrounded by a layer of muscle fibers oriented dorso-ventrally.

The genito-intestinal canal arises laterally from the dorso-lateral wall of the female antrum. It reaches the intestine by passing dorsally and to the right of the seminal vesicle. It is attenuated in passing around the seminal vesicle, thus no details of its structure could be discerned.

The mass of the germovitellarium consists of developing follicles. In the posterior, immature follicles the ova are surrounded by accessory cells, which stain deeply with hematoxylin. More mature, anterior follicles, containing ova 35μ-40μ in diameter, consist of large accessory cells with eosinophilic cytoplasm and prominent nuclei, up to 12μ in diameter.

Taxonomic diagnosis.—In the only comprehensive treatment of the family Prorhynchidae, Steinböck (1927) created a second genus in the family by resurrecting the name *Geocentrophora* de Man. Into this genus he transferred *Prorhynchus sphyrocephalus* de Man, *P. balticus* Kennel, *P. applanatus* Kennel and *P. metameroides* Beauchamp. In the same work he declared *Prorhynchus curvistylus* M. Braun, *P. hygrophilus* Vejdovsky and *P. leuckarti* Zacharias to be conspecific with *Geocentrophora sphyrocephala,* thus reducing the number of European species of *Geocentrophora* to two, *G. sphyrocephala* and *G. baltica.* His inclusion of the American species *Geocentrophora applanata* and *G. metameroides* in *Geocentrophora* was based merely on external similarities, since the male reproductive systems to which the generic

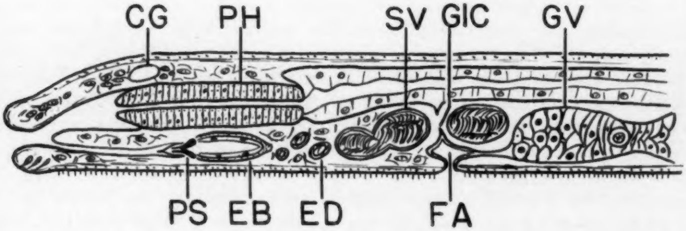


Fig. 19.—Mid-sagittal section of the anterior half of *Geocentrophora marcusi.* See Figs. 5-6 for explanation of abbreviations.

diagnoses refer were not known at that time. Although the male system of *G. metameroides* has not yet been described, that of *G. applanata* has (Jones, 1929). This, as well as the corroborative evidence of Marcus (1944), indicated that it was correctly placed by Steinböck in *Geocentrophora*. Hyman (1941) added a fifth species, *Geocentrophora tropica,* but stated that she did not consider as adequate the grounds for transferring *Prorhynchus applanatus* and *P. metameroides* to *Geocentrophora.*

In this paper the definition of *Geocentrophora* used is that given by Steinböck (1927:635). It is considered as including, in addition to *Geocentrophora marcusi,* two European species, *G. sphyrocephala* and *G. baltica,* and three American species, *G. applanata, G. metameroides* and *G. tropica.* The two species known only from tropical America, *Geocentrophora tropica* and *G. metameroides,* do not show close similarity with each other nor with other members of the genus. *Geocentrophora metameroides,* taken from Bromeliad-leaf pools in Costa Rica, is insufficiently known since its male system has not been described. Yet, several characters set it off from other species of the genus, including *G. marcusi*: it lacks eyes and ciliated pits, has a germovitellarium bearing diverticula and a brain situated more posterior with respect to the pharynx. The largest of the American species, *Geocentrophora tropica,* 5 mm long when preserved, was collected from the forest floor on Barro Colorado Island, Canal Zone. It is eyeless and is unique in having only two pairs of testicular follicles, black pigmentation, and an extremely curved penis stylet.

Geocentrophora applanata is the only American species known to have a wide distribution: New York, Virginia, Trinidad, and Brazil. In size and body form it resembles *G. marcusi* but lacks the prominent, tapering auricles of the Georgia worm. Also, the male system has several features which differ from those of *G. marcusi*: the seminal vesicle lies more anterior in *G. applanata,* and the testicular follicles number only three to six pairs. The digestive system of *G. applanata* is characterized by elongate, intestinal diverticula and a central pharyngeal sphincter (Kennel 1888). In *Geocentrophora marcusi* the pharyngeal sphincter is not present nor are the intestinal diverticula elongate.

Geocentrophora sphyrocephala occurs in Eurasia from France to Turkistan, and from Bulgaria to the Scandinavian and Kola peninsulas and the Faroes Islands (Graff, 1913:62; Steinböck, 1927:627; 1931). Porter (1936, unpublished) recorded it from western Virginia. Mature specimens range in length from 0.6 mm to 5 mm. The head, bearing pointed auricles, resembles that of *G. marcusi* more than do other species, however, the body differs in having an oval shape and a tapering posterior end. With regard to the male system, *Geocentrophora marcusi* differs from *G. sphyrocephala* in having a less sharply curved penis stylet, a seminal vesicle four to six times as large and more posterior in position, and in having fourteen to twenty pairs of testicular follicles in contrast to three to six pairs in the European

worm. The female systems differ in that the genito-intestinal canal in *G. marcusi* is connected to the female antrum and not to the oviduct as in *G. sphyrocephala.* Two features of the digestive systems of the two worms are different; *G. marcusi* has distinct intestinal diverticula rather than the crenated appearance of *G. sphyrocephala,* also the Georgia prorhynchid lacks the pharyngeal sphincter present in *G. sphyrocephala.*

The largest species of the genus, *Geocentrophora baltica,* has been reported from Germany to Turkistan and from Bulgaria to the Kola Peninsula (Steinböck, 1927:660). It is reported by Porter (1936, unpublished) as also occurring in western Virginia. Its body form is ribbon-like with a spatulate head, lacking eyes, and an abruptly tapered posterior end. It is unique in having the penis anterior to the brain which in turn is anterior to the pharynx. The male system resembles that of *G. marcusi* in several respects: the shape of the penis stylet, the large size (250μ long) of the seminal vesicle, and the large number of testicular follicles (fourteen to sixteen pairs). The female systems of the two worms differ in that *G. baltica,* like *G. sphyro*-cephala, has the genito-intestinal canal connected to the oviduct in contrast to the antral connection in *G. marcusi.* The pharynx of *G. baltica* is similar to that of the Georgia prohynchid in size and in lacking a muscular sphincter. Although obvious differences exist between *G. marcusi* and *G. baltica,* the similarities in the anatomy of the male reproductive systems suggest that *G. marcusi* is more closely related to it than to other members of the genus.

Differential diagnosis.—Characteristics of *Geocentrophora marcusi* which distinguish it from all other species of the genus are: red eyes, red body pigment, prominent auricles, and a genito-intestinal canal connected to the female antrum. Also, it differs from *G. tropica* in having a less-curved penis stylet and in having fourteen to twenty-four pairs of testicular follicles rather than two pairs; from *G. applanata* and *G. sphyrocephala* in having a larger seminal vesicle, which is more anterior in position, and in having fourteen to twenty-four pairs of testicular follicles rather than three to six pairs; from *G. baltica* in having a truncate posterior end and in having the penis, brain, and pharynx occurring at the same anterior-posterior level of the body.

Type material.—The type material of *Geocentrophora marcusi* is deposited in the United States National Museum: *holotype,* whole mount USNM 29736; one *paratype,* serial sagittal sections (one slide) USNM 29737; one *paratype,* serial transverse sections (two slides) USNM 29738. The type locality is Mt. Panola, Rockdale Co., Georgia. This species is named for Professor Ernesto Marcus of the University of Sao Paulo whose researches have contributed greatly to the knowledge of Turbellaria, particularly in South America.

Observations on living Geocentrophora marcusi.—Sexually mature specimens were collected throughout the winter from November 27 until March 25. They were found only at Mount Panola, occurring in the pools at or near the summit of the outcrop. Usually several

hours collecting yielded only six or eight specimens. In only one instance were they found in abundance; some fifty individuals in a runoff rivulet were attracted from under gravel substrate by baiting with a crushed insect several inches upstream.

This species has the ability to roll into a spherical shape, its dorsal surface exposed, and form a transparent enveloping cyst. Two other species of the genus, *G. baltica* and *G. sphyrocephala,* are known to have the same ability. *Geocentrophora baltica* is said to over-winter in the encysted condition (Graff, 1913:51), and Sekera (in Steinböck, 1927:651) stated that this worm lived in damp moss and leaves, and will encyst not only in response to drying but also if submerged in a large amount of water.

Encysted and active specimens of *Geocentrophora marcusi* were seen to occur simultaneously in the same pools and rivulets. They frequently encysted in the laboratory. They would often encyst following agitation of the water or the placing of food near them. In the laboratory one specimen was observed to have formed a cyst within ten minutes after rolling into a spherical shape. Encystment apparently gives some protection against drying in this Georgia prorhynchid also, for the damp substrate of a pool, from which the water had disappeared, produced two mature specimens within twenty-four hours after being covered with water in the laboratory. Whether or not encysted specimens of *G. marcusi* can withstand desiccation sufficient to enable them to over-summer was not clearly demonstrated. Dried substrate from an outcrop pool did produce one specimen twenty days after being covered with water in the laboratory; however, development from an egg cannot be eliminated as a possible explanation of this appearance, since embryological development in related species is reported as requiring only ten days to three weeks (Steinböck, 1927:651; Graff, 1913:61).

The gliding movement of *G. marcusi* is relatively rapid; when moving, the head is turned from side to side in a quivering motion. It was not observed to feed in nature except on injured Collembola used as bait. In the laboratory it fed on beef liver, injured insect larvae, and injured amphipods. Eggs of this species were never seen nor was copulation observed.

DISCUSSION

Since the systematics of each worm is presented separately, the discussion is concerned primarily with general aspects of their ecology.

The apparent endemism of the Turbellaria described here and the absence of other Turbellaria from the granite pools is particularly interesting. Collecting in the area surrounding the outcrops indicated that the three new species were restricted to the outcrops. This, however, cannot be regarded as definite since a widespread survey of the turbellarian fauna of northern Georgia has not been made. As to the restricted nature of the turbellarian fauna of the granite pools, the information is almost conclusive. On only three occasions were Turbel-

laria other than the new species described here found. In one collection two specimens of *Macrostomum* sp. were taken; in another, approximately ten specimens of *Castrella* sp.; and in a third instance, three specimens of a triclad resembling most closely *Phagocata velata* (Stringer) were found. The latter was not present in pools on the granite slopes but in pools at the base of the outcrops. Since each of these three species was taken only once in spite of numerous collections, it is likely that they represent accidental intruders which could maintain themselves temporarily in the pools but could not survive there from season to season. It is to be noted that of the three new species of Turbellaria which are successful in the rigorous environment of the outcrops, each represents a different one of the three fresh-water orders of the class.

Environmental conditions in the granite pools which would seem to require of the inhabitants unusual tolerance or adaptations are two: first, low temperatures with large daily fluctuations; second, seasonal desiccation accompanied by high temperatures. Species of *Geocentrophora* in general tolerate varying conditions of moisture better than most other groups of Turbellaria; this is due at least in part to their ability to encyst (Steinböck, 1927:626). It is probable that the encysting ability of *G. marcusi* is of particular value in enabling it to withstand the special conditions of the outcrop pools; however, there is no evidence as to whether or not encysted individuals can survive the summer desiccation. It seems more probable that season to season survival depends upon a resistant type egg.

The characteristics of *Mesostoma georgianum* in relation to the apparent exigencies of the environment seem more obvious. Individuals are active throughout a wide range of temperatures; on several occasions they were observed to be normally active in pools which were covered with ice. There was no evidence that they can encyst; indeed, there is only scant evidence that any member of the genus can. Meixner's report (1915) of encystment of *Mesostoma lingua* in Alpine pools is not conclusive. The production of resistant eggs exclusively would seem to have definite survival value in the granite-pool habitat. Most other species of *Mesostoma* produce less resistant, quickly-hatching eggs in the early part of the growing season, and resistant eggs towards the end of the season. The first type increases the population during the growing season; the second type ensures its survival into the next season. The production of only the resistant type egg would seem to ensure *Mesostoma georgianum* the season-to-season survival of the species at the expense of total numbers during one growing season. The ability of *M. georgianum* to capture the semi-aquatic Collembola is not only interesting as an unusual kind of predation for an aquatic turbellarian, but also seems intimately connected with the maintenance of its large populations. The Collembola appear to be the most numerous of any of the groups making up the macrofauna of the pools; in addition, their appearance during the year parallels that of the mesostomine worms. In being able to

use this relatively constant and abundant source of food, the worms have sufficient nourishment to permit rapid maturation and an extended period of egg production.

Mesostoma georgianum, unlike most other Turbellaria, does not exhibit an avoiding reaction to light. This behavior is a prerequisite to their capturing collembolans in the daytime since these insects are available to the worms only when they are on the open surfaces of the pools. The worm's dense pigmentation may be related to its unusual behavior in light. Ruebush (1939) has suggested that the density of pigmentation in species of *Mesostoma* is related to a shallow pool habitat at high altitudes. Three darkly pigmented species of *Mesostoma,* described by him from Tibet, were found in pools at altitudes of 12,000 feet to 15,000 feet. *Mesostoma lingua,* the most characteristic turbellarian of the Alpine pools according to Brehm and Ruttner (1926), was described by Fuhrmann (in Klausner, 1908) as being more darkly pigmented the higher the altitude of its habitat. In the United States the two darkly pigmented species, *Mesostoma virginianum* and *M. macroprostatum,* likewise are montane forms; the former was collected at 3,500 feet in Virginia, the latter at 5,000 feet in Wyoming. The density of pigment in the Georgia worm is equal to that of these other montane species, however, the altitudes of the habitat are vastly different. This suggests that the dense pigmentation of *Mesostoma georgianum,* as well as that of the other mountain-dwelling forms, may be as much related to the exposed condition of the habitat as it is to the altitude.

The survival of *Phagocata bursaperforata* in the granite-pool habitat is perplexing in view of the fact that it exhibits characters usually associated with cave-dwelling forms — the absence of eyes and the lack of body pigmentation. The contrasting conditions of the two environments and the fact that no caves are known on or in the vicinity of the outcrops precludes the possibility that this worm is an escapee from a cave. Species of blind, white, cavernicolous triclads are numerous in the mountains of central Europe and the Karst region of the Balkans (Komarek, 1920; Beauchamp, 1932; Kenk, 1935). The European triclads *Planaria torva* (O. F. Muller) and *Crenobia montenigrina* (Mrazek), known first as pigmented, eyed, epigean species, were later found to have hypogean varieties lacking body pigment and having degenerate eyes. Nevertheless, the association of the lack of eyes and body pigment with a spelean habit is not absolute.

Dendrocoelum Mrazeki (Vejdovsky), a European species lacking eyes and body pigment, is epigean, whereas *Sorocelis americana* Hyman, a cave species from Oklahoma, lacks body pigment but has eyes (Hyman, 1939c). Also, *Procotyla typhlops* Kenk, a white, epigean triclad, is known to occur with and without eyes (Hyman, 1945). Hyman (1939c) considered the multiocular condition of the epigean species *Phagocata morgani* var. *polycelis* Kenk as evidence of a ten-

dency towards degeneration of eyes in the genus. The eyeless condition of *Phagocata bursaperforata* may be the result of such a tendency.

In discussing the systematic relationships of the family Kenkiidae, which consists of cave-dwelling forms exclusively, Hyman (1937b) suggested that the group was derived from the genus *Phagocata.* The primary basis for the suggestion was the close similarity of the copulatory organs in the two groups. As supplementary evidence she mentioned the absence of body pigment in certain species of *Phagocata* and the tendency towards degenerate eyes in *P. morgani* var. *polycelis* as noted above. *Phagocata bursaperforata* could be considered as evidence in support of Hyman's suggestion. Not only does it resemble the Kenkiidae with respect to the copulatory organs, body pigmentations, and the absence of eyes, but it also has as a character in common, prepharyngeal testes. *Phagocata vernalis* Kenk is the only other American member of the genus having a distribution of testes similar to the members of the Kenkiidae, and it has both eyes and body pigment (Kenk, 1944).

SUMMARY

The pools characteristic of Stone Mountain and similar granite outcrops near Atlanta, Georgia have, from November to April, a turbellarian fauna consisting almost exclusively of three new species, each from a different one of the three fresh-water orders.

The rhabdocoele is *Mesostoma georgianum,* a black, cigar-shaped form which is by far the most abundant. The large populations of this species are in part maintained by its unusual ability to prey upon the numerous collembolans and upon its production of resistant eggs, which remain viable in spite of extreme heat and desiccation during the summer. Serially sectioned specimens form the basis for the study of the internal morphology; also, observations on the reproductive behavior were reported, as well as studies based upon specimens sectioned *in copula.* On the basis of internal morphology an affinity with *Mesostoma macroprostatum* Hyman is indicated.

The order Tricladida is represented by a slender, white form, *Phagocata bursaperforata,* in which the lack of eyes and of body pigment resemble hypogean species. From the morphology of the reproductive system it is suggested that this triclad is related to *Phagocata morgani* (Stevens and Boring).

The order Alloeocoela is represented by the prorhynchid worm, *Geocentrophora marcusi,* a small, red-pigmented form found only on Mt. Panola. Serial section studies form the basis for the description of the internal morphology; laboratory observations on its ability to encyst are presented.

Certain features of these new species — pigmentation, reproduction, encystment — are discussed with regard to their possible survival value in the unusual habitat of the granite outcrop pools.

REFERENCES

BEAUCHAMP, P. DE 1929—Nouvelles diagnoses de Triclades obscuricoles. Bull. Soc. zool. Fr. **53**:510-513, fig. 1.

———1932—Turbellariés, Hirudinées, Branchiobdellidés, Biospeologica LVIII. Arch. Zool. exp. gén. **73**:113-380, figs. 1-55, pls. VI-VIII.

———1937—Nouvelles Diagnoses de Triclades obscuricoles. Bull. Soc. Zool. Fr. **62**:265-271, figs. 1-3.

———1939—La systematique et l'ethologie des *Fonticola* (Turb. Triclades). Vestnik. ceskosl. zool. Spolec. **6-7**:91-96.

———1940—Études Biospéologiques. XX(I). Triclades Obscuricoles de Roumanie. Bull. Mus. Hist. nat. Belg. **56**(16):1-5.

BREHM, V. AND F. RUTTNER 1926—Die Biocönosen der Lunzer Gewässer. Int. Rev. Hydrobiol. **16**(5/6):281-391.

BRESSLAU, E. 1933—*In*: Kükenthal und Krumbach, Handbuch der Zoologie, Bd. II, Vermes Amera. Plathelminthes.

COSTELLO, D. P. AND H. M. COSTELLO 1938—Copulation in the Acoelous Turbellarian *Polychoerus carmelensis*. Biol. Bull. **75**(1):85-98, figs. 1-3, pls. I-II.

DAHM, A. G. 1949—*Phagocata* (= *Fonticola*) from South Sweden (Turbellaria Tricladida Paludicola) taxonomical, ecological and chorological studies. Acta Univ. Lund **45**(7):1-32, figs. 1-7.

FERGUSON, F. F. AND W. J. HAYES, JR. 1941—A synopsis of the genus *Mesostoma* Ehrenberg 1835. J. Elisha Mitchell Sci. Soc. **57**(1):1-52, figs. 1-20.

GELEI, J. V. 1933—Plankton-und Warmwasser-Turbellarien in den ungarländischen Gewässern. Zugleich ein Beitrag zur Morphologie von *Mesostoma productum* O. Schm. Zool. Jahrb. **64**:111-128, figs. 1-4.

GRAFF, L. V. 1913—Das Tierreich. Turbellaria II. Rhabdocoelida. 35 Lieferung, pp. xix+484, 394 figs., Berlin.

HUSTED, L. AND T. K. RUEBUSH 1940—A comparative cytological and morphological study of *Mesostoma ehrenbergii ehrenbergii* and *Mesostoma ehrenbergii wardii*. J. Morph. **67**(3):387-409, figs. 1-16.

HYMAN, L. H. 1925—The reproductive system and other characters of *Planaria dorotocephala*. Trans. Amer. Micr. Soc. **44**(2):51-82, figs. 1-2, pls. I-III.

———1937a—Reproductive system and copulation in *Amphiscolops langerhansi* (Turbellaria Acoela). Biol. Bull. **72**(1):319-326, figs. 1-7.

———1937b—Studies on the morphology, taxonomy and distribution of the North American Turbellaria. VIII. Some cave planarians of the United States. Trans. Amer. Micr. Soc. **56**:457-477, pls. I-III.

———1937c—Studies on the morphology, taxonomy and distribution of the North American Turbellaria. VII. The two species confused under the name *Phagocata gracilis*, the validity of the generic name *Phagocata* Leidy, and its priority over Komarek 1926. Trans. Amer. Micr. Soc. **56**(3):298-310, figs. 1-5.

———1938—North American Rhabdocoela and Alloeocoela. III. *Mesostoma arctica*, new species. Amer. Mus. Nov. **1005**:1-8, figs. 1-6.

———1939a—North American Rhabdocoela and Alloeocoela. V. Two new Mesostomine Rhabdocoels. Amer. Midl. Nat. **22**(3):629-636, figs. 1-8.

———1939b—North American Rhabdocoela and Alloeocoela. IV. *Mesostoma macropenis*, new species, from Douglas Lake, Michigan. Amer. Midl. Nat. **21**(3):646-650, figs. 1-4.

———1939c—North American Triclad Turbellaria. X. Additional species of cave planarians. Trans. Amer. Micr. Soc. **58**(3):276-284, figs. 1-9, pls. I-II.

———1941—Terrestrial flatworms from the Canal Zone, Panama. Amer. Mus. Nov. **1105**:1-11, figs. 1-15.

———1945—North American Triclad Turbellaria. XI. New, chiefly cavernicolous planarians. Amer. Midl Nat. **34**(2):475-484, figs. 1-8.

———1951a—The Invertebrates: Platyhelminthes and Rhynchocoela. Vol. II. New York: McGraw-Hill Book Co., vii+550, 208 figs.

———1951b—North American Triclad Turbellaria. XII. Synopsis of the known species of fresh-water planarians of North America. Trans. Amer. Micr. Soc. **70**(2):154-166.

IJIMA, ISAO AND TOKIÖ KABURAKI 1916—Preliminary descriptions of some Japanese Triclads. Annot. Zool. Jap. **9**:153-171, figs. 1-24.

JONES, E. R., JR. 1929—The male reproductive system of the turbellarian *Prorhynchus applanatus* Kennel. Trans. Amer. Micr. Soc. **48**(1):70-72, pl. XII.

KEEVER, C., H. J. OOSTING AND L. E. ANDERSON 1951—Plant succession on exposed granite of Rocky Face Mountain, Alexander County, North Carolina. Bull. Torrey Bot. Club **78**:401-421.

KENK, ROMAN 1930a—Beiträge zum System der Probursalier (Tricladida Paludicola). I and II. Zool. Anz. **89**(5/6):145-162, figs. 1-3.

———1930b—Beiträge zum System der Probursalier (Tricladida Paludicola). III. Zool. Anz. **89**(11/12):289-302.

———1932—A convenient method of photographing small animals at low magnification. Science **75**(1956):669-670.

———1935—Die Höhlentricladen Slovenien. Verh. int. Vereinig. Limnol. **7**:87-91.

———1936—Eine neue Höhlentriclade, *Fonticola opisthogona* n. sp. Zool. Anz. **113**:305-314, figs. 1-3.

———1937—Eine neue Süsswassertriklade aus der Umgebung von Graz, *Fonticola prosorchis* n. sp. Zool. Anz. **117**(1/2):43-48, figs. 1-3.

———1944—The fresh-water triclads of Michigan. Univ. Michigan Mus. Zool. Misc. Pub. **60**:1-44, figs. 1-5, pls. I-VII.

KENNEL, J. 1888—Untersuchungen an neuen Turbellarien. Zool. Jahrb. Abt. f. Anat. **3**:447-486, pls. XVIII-XIX.

KLAUSENER, CARL 1908—Die Blutseen der Hochalpen. Int. Rev. Hydrobiol. **1**:359-424.

KOMAREK, JULIUS 1920—Über höhlenbewohnende Tricladen der balkanischen Karste. Archiv. Hydrobiol. **12**:822-828.

LUTHER, A. 1904—Die Eumesostominen. Z. wiss. Zool. **77**:1-273, pls. I-IX.

MAKINO, SAJIRO 1951—An atlas of the chromosome numbers in animals. Ames, Iowa: The State College Press, pp. xxvii+290.

MARCUS, ERNESTO 1944—Sôbre duas Prorhynchidae (Turbellaria) para o Brasil. Arg. Mus. Paranaeuse **4**(1):1-45, pls. I-II.

MARCUS, EVELINE DU BOIS-RAYMOND 1951—Two fresh-water Turbellaria from Natal. Ann. Natal Mus. **12**(1):73-80, figs. 1-9.

MEIXNER, JOSEF 1915—Zur Turbellarienfauna der Ost-Alpen, insonderheit des Lunzer Seengebietes. Zool. Jahrb. **38**.

———1928—Die Genitalapparat der Tricladen und Seine Bezeihungen zu ihrer Allgemeinen Morphologie, Phylogenie, Ökologie und Verbreitung. Z. Morph. Ökol. Tiere **11**:570-612, figs. 1-18.

OKUGAWA, K. 1939—Probursalia (Triclada-Paludicola) of Manchoukuo. Annot. zool. jap. **18**:155-164, figs. 1-6, pls. I-VII.

PAPI, FRANCISCO 1949—Il ciclo Biologica di *Mesostoma benazzi* Papi (Neorhabdocoela: Typhloplanidae). Boll. Zool. **16**(1/3):41-48.

PORTER, RICHARD J. The family Prorhynchidae in America. Unpublished Master's thesis, Department of Biology, University of Virginia, 1936.

RUEBUSH, TRENTON K. 1939—Report on the Rhabdocoele Turbellaria collected by the Yale North India Expedition. Zool. Anz. **126**(3/4):49-67, figs. 1-6.

STEINBÖCK, OTTO 1927—Monographie der Prorhynchidae (Turbellaria). Z. Morph. Ökol. Tiere **9**(3/4):538-662, figs. 1-40.

———1931—Fresh-water Turbellaria. Zoology of the Faroes. Copenhagen.

WEISS, ANNIE 1910—Beiträge zur Kenntnis der australischen Turbellarien. Z. wiss. Zool. **96**:336-372, figs. 1-13.

Experimental and Natural Hybridization between Bufo terrestris and Bufo fowleri[1]

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In analysing populations in which interspecific hybridization is suspected, the systematist seeks out the similarities and dissimilarities between the parental species. The alleged hybrids are then evaluated in terms of the differential characters of the two species. Determining which and how many of the character differences are to be selected as criteria of hybridization constitutes the critical phase of the procedure.

Two species may differ so widely that individuals of one group are readily separable from the other. The differences may relate to the presence or absence of several qualitative characters. Some of the quantitative characters may display no or little overlapping of values when the measurements are plotted. In this case, a "hybrid index" method (Anderson, 1936, 1949; Hubbs and Hubbs, 1943) may be employed and it may be safely inferred that individuals with intermediate values represent products of hybridization. In other cases, the differences between two species may be such that there is considerable overlap when the values for any single character are plotted. *Bufo terrestris* and *Bufo fowleri* are two such entities. Few of the morphological differences between them are absolute, in the sense that one species possesses a characteristic that the other entirely lacks. A unique morphological feature of *B. terrestris* is the knob-like swellings on the posterior ends of the interorbital cranial crests. For the most part, however, the differences between *B. terrestris* and *B. fowleri* are ones of degrees. The two toad species differ in the size and distribution of warts, the extent of ventral spotting, the shape and coloration of the parotoid glands, the configuration of the snout, and other variable quantitative traits. These characters overlap broadly. The paucity of well-defined morphological differentials between the two species renders difficult the detection of hybridization in sympatric areas. Convincing data requires the demonstration that experimental hybrids between the two species resemble individuals collected in mixed breeding aggregations.

The data reported herein deal with the success attained in reconstructing experimentally the suspected natural hybridization between *B. terrestris* and *B. fowleri* in southeastern Louisiana and adjacent Mississippi. Controlled cross-breeding experiments revealed the morphological features of hybrid individuals, as well as provided the

[1] This investigation was supported by a grant from the National Science Foundation (NSF-G3332).

requisite information as to the particular characteristics that could or could not be employed as valid indices of hybridization. Several natural populations were then analyzed in terms of the experimentally-determined characters to estimate the existence and extent of hybridization in each population. Some hybrid populations exhibit a wide diversity of character recombinations of the two species ("hybrid swarms"); others apparently represent the outcome of repeated back-crossing of hybrids to one or the other parental species.

BACKGROUND OF THE PROBLEM

The total ranges of the two species and their distribution in Louisiana and southern Mississippi are plotted in Figure 1. *B. fowleri* occupies most of the eastern half of the United States; *B. terrestris* inhabits the southeastern corner of the United States. The ranges of the two species overlap in a narrow zone extending from North Carolina to Louisiana.

The distributional patterns in Louisiana and southern Mississippi were determined from locality records contained in the amphibian collections at Tulane University and at Louisiana State University. The map is to be considered as tentative and serves solely as an operational framework of reference. It is not intended in its present form to reveal anything of the character of the populations except that the two species are known to inhabit the respective regions represented. The "lettered" populations refer to those analyzed, and will be considered later.

B. terrestris extends into the southeastern parishes of Louisiana, east of the Mississippi River. Members of this species are commonly identified solely on the basis of the terminal swellings of the inter-

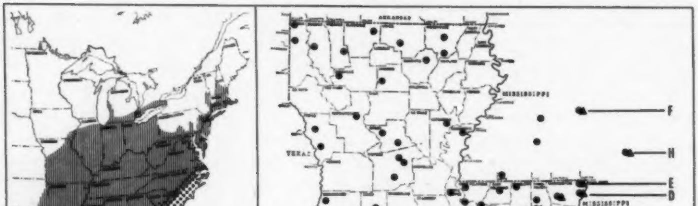

Fig. 1.—Left: Approximate ranges of *Bufo fowleri* (vertical lines) and *Bufo terrestris* (squares). Right: Locality records of *B. fowleri* (dots) and *B. terrestris* (triangles) in Louisiana and southern Mississippi. Character analyses of populations A-G are represented in Fig. 4.

orbital cranial crests. In southeastern Louisiana and adjacent Mississippi, continuous variation in this component may be found, ranging from a club-shaped prominence to a small, slightly swollen projection. Whether the latter is an extreme variant condition or one modified by hybridization has been a question posed by various investigators familiar with the bufonid fauna of Louisiana.

The more problematic entity in Louisiana is *B. fowleri*. Dissatisfaction with the status of this species in the Gulf states is evident in the writings of several investigators (Anderson, Liner, and Etheridge, 1952; Blair, 1941, 1947; Bragg, 1955; Bragg and Sanders, 1951; and Volpe, 1953). In the eastern portion of its range in the United States (along the Atlantic coast), *B. fowleri* is characterized by small rounded warts, no preparotoid ridge (connecting the postorbital crest with the parotoid gland), and an unspotted venter. Individuals resembling the eastern seaboard form may be found in Louisiana, but many differ markedly from the typical description of *B. fowleri*. Individuals with large spinous warts, preparotoid connections, and venters mottled to varying degrees are of common occurrence in Louisiana populations. Bragg and Sanders (1951) actually designated a group of *fowleri*-like toads with intense ventral spotting from eastern Texas and northeastern Louisiana as a new subspecies.[2] A. P. Blair has been more conservative in his analysis of toads of the Gulf states, as evidenced by his cautious statement (1947, p. 4), "The writer has in the past referred to the toads of the lower Mississippi valley as *B. fowleri* and this is perhaps the best designation."

Since the populations of *B. fowleri* are located at the outer limits of the vast range of the species, it may be surmised that the extreme populations of the species are differentiating along new and separate lines. Volpe (1953, 1957a) found that *B. fowleri* from southeastern Louisiana differ in embryonic temperature adaptations from their counterpart along the Atlantic coast. No geographical variation, with respect to the embryological characters studied, was found among the eastern seaboard *B. fowleri* (New York, New Jersey, North Carolina, and South Carolina). It could not be deduced, however, from the data whether or not the differences observed in Louisiana *B. fowleri* reflect differential physiological adaptations to regional environmental conditions or are traceable to the effects of past hybridization with *B. terrestris*.

The possibility of hybrid influences in Louisiana *B. fowleri* populations cannot be discounted on the basis of any known isolating mechanism. The mating calls of the males of *B. terrestris* and *B. fowleri* are of little significance in maintaining isolation. The mating reaction is apparently non-specific; males of one species will clasp readily females of either species both in the laboratory and in nature. Mixed

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[2] *Bufo fowleri* is commonly referred to as *Bufo woodhousei fowleri;* accordingly, Bragg and Sanders designated the new subspecies as *B. woodhousei velatus.*

breeding aggregations and mis-mated pairs have been observed by the writer and members of the Tulane field crew. There are no detectable differences in breeding periods; each species breeds continuously in Louisiana from late March to late July.

The data of the present investigation indicate that *B. fowleri* populations in southeastern Louisiana and adjacent Mississippi have been modified by hybridization with *B. terrestris*.[3] Although the results pertain to populations in the area of overlap of the two species, the data do shed some light on the problematic *B. fowleri* populations outside of the area of contemporary contact (i.e., in western Louisiana).

BREEDING EXPERIMENTS

Adults of each species collected by the author, or obtained from colleagues during the spring months of 1954-1957, were crossed in various combinations in the laboratory. The experimental procedures were similar to those employed in earlier work of this type (Volpe, 1954). A preliminary series of hybrid crosses, *terrestris* ♀ X *fowleri* ♂ (two experiments) and *fowleri* ♀ X *terrestris* ♂ (three experiments), carried out in 1954, confirmed A. P. Blair's finding (1941, 1942) that the hybrid embryos are viable. No marked developmental irregularities were noted in the reciprocal hybrids during early embryonic development. These experiments were terminated when the larvae reached the gill circulation stage (stage 20; defined in Pollister and Moore, 1937).

In the experiments performed during 1955-57, the offspring from each cross were raised beyond metamorphosis. Tadpoles were reared in shallow enamel pans containing pond water and spinach. The metamorphosed toads were fed vestigial-winged fruit flies, meal worm larvae, and pieces of liver dipped in bone meal. The snout-to-vent lengths of transformed toads ranged from 8.5 to 10.5 mm. Newly-metamorphosed toads exhibit a dorsal pattern of warts and a median dorsal stripe, but lack three cardinal features of the adults — the parotoid glands, the tympana, and the cranial crests. The parotoid glands are present in varied degrees of distinctness in 15-20 mm toads. The tympana are first noticeable in the 20-25 mm size range. The precursors of the cranial ridges consist of fine rows of tubercles, barely visible in 20-25 mm toads. The ridges are discernible in the 25-30 mm size group, and usually distinct in the 30-35 mm group.

Mortality is considerable in young toads maintained under laboratory conditions. From eight to thirteen offspring were reared beyond a size of 30 mm in each of the crosses discussed below. No success was attained in rearing the offspring of any cross to sexual maturity. The

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[3] *B. fowleri* encompasses both the ranges of *B. terrestris* and *B. valliceps* in Louisiana. Although hybridization between *B. fowleri* and *B. valliceps* does occur, the evolutionary effects are essentially negative. The hybrids are either inviable or sterile males (Volpe, 1956, 1957b).

TABLE I.—Segregation of cranial crest components in an F_1 hybrid between *Bufo terrestris* and *Bufo fowleri*

Components	*B. terrestris*	*B. fowleri*	F_1 Hybrid
Interorbitals (between orbits)	Divergent from nostrils; club-like terminal prominences.	Parallel to each other; no terminal prominences.	Slightly divergent; terminal prominences reduced to short projections.
Postorbitals (below orbits)	Meet interorbitals at an angle greater than 90°.	Meet interorbitals at right angles.	Meet interorbitals at an angle slightly greater than 90°.
Preorbitals (above orbits)	Distinct.	Relatively weakly developed.	Distinct.
Preparotoids (between parotoid gland and postorbital crest)	Conspicuous connecting ridge.	Absent (parotoid gland in direct contact with postorbital).	Prominent, relatively short connective.
Supratympanics (between tympanum and orbit)	Well-defined.	Relatively weakly developed.	Well-defined.

crosses consist of three experimental sets; the results of each set shed light on a particular aspect of the problem.

EXPERIMENTAL SET I

B. terrestris ♀ (Dunedin, Fla.) X *B. terrestris* ♂ (Dunedin, Fla.)
X *B. fowleri* ♂ (Brooklyn, N. Y.)
B. fowleri ♀ (Brooklyn, N. Y.) X *B. fowleri* ♂ (Brooklyn, N. Y.)
X *B. terrestris* ♂ (Dunedin, Fla.)

The adults used in these reciprocal crosses were obtained[4] from populations outside the distributional overlap of the two species (Fig. 1). The objective was to ascertain the segregation of traits in F_1 hybrids derived from parents that unquestionably represented "pure" members of each species. The characteristics of the parental forms and the F_1 hybrid from the cross, *B. fowleri* ♀ X *B. terrestris* ♂, are illustrated in Figure 2; data on the segregation of the cranial crest components are given in Table I.

The divergent, elevated interorbital (supraorbital) cranial crests terminating posteriorly in inwardly-curved knobs constitute the most

[4] The writer is grateful to Dr. Max Hecht for supplying the *fowleri* individuals from New York.

conspicuous characteristic of *terrestris*. In contrast, the interorbitals in *fowleri* are parallel, relatively non-elevated, and do not end posteriorly in club-shaped prominences. Large spinous warts and the presence of a preparotoid ridge connecting the parotoid gland with the postorbital crest are other major features that distinguish *terrestris* from *fowleri*. Typical *fowleri* individuals have small, rounded warts and the parotoids are in direct contact with the postorbital cranial ridges. The extent of ventral markings in *terrestris* individuals varies from an unspotted (omitting the black throat of the male) to a heavily reticulated condition. Between these extremes are the single pectoral spot and various gradations of pectoral-abdominal spotting. The *terrestris* male used in the hybrid cross (Fig. 2) was especially chosen for his mottled venter. This extreme condition contrasts sharply with the immaculate venter of the *fowleri* female employed in the cross. *B. fowleri* individuals from the eastern states (along the Atlantic seaboard) typically are unmarked ventrally or possess a single pectoral spot.

Nine offspring from the *B. fowleri* ♀ X *B. terrestris* ♂ cross were reared successfully beyond metamorphosis. The F_1 hybrid illustrated (Fig. 2) is a 39 mm female. The hybrid is intermediate in certain characteristics but resembles one or the other parental species in other traits. The prominent knobs of the interorbitals of the *terrestris* parent are modified in the hybrid as short, inwardly-curved, slightly raised projections. The parotoid gland of the hybrid is connected to the postorbital crest by a ridge that is structurally similar to, but shorter than, the preparotoid ridge of the *terrestris* parent. The ventral surface is spotted in all hybrids; the spotting is more or less confined to the pectoral region. The warts on the back and legs of the hybrids tend to be more spinous than those found in the *fowleri* parent. The dorsal black spots of the hybrid illustrated are arranged differently from those of the parents. However, there is no consistent pattern; the arrangement of dorsal spots is highly variable among the hybrids. The hybrids resemble the *fowleri* parent with respect to the configuration of the parotoid glands (long and narrow) and the shape of the snout (short and blunt).

In the cross, *B. terrestris* ♀ X *B. fowleri* ♂, the components of the cranial crests segregated in the F_1 hybrids in a manner identical to the aforementioned cross (Table I). The ventral surface of the *terrestris* male used in this cross contained a median pectoral spot and a few markings adjacent to it. The *fowleri* parent possessed only a single median spot. The nine hybrids recovered did not exceed either parent in the amount of ventral spotting. The parotoid glands are shaped more like the *fowleri* than the *terrestris* parent. In general, the appearance of the hybrids tends more in the direction of the *fowleri* than of the *terrestris* parent.

The data from the reciprocal crosses may be summarized as follows: The most notable modification in the F_1 hybrid occurs in the cranial crest components. Many of the warts appear to be interme-

diate in size, but this is difficult to judge objectively. Ventral spotting is governed apparently by a complex of genes, or polygenes; the extent of ventral markings in the hybrid depends upon the number of spotting genes present in the given parents. The character which appears to be strongly influenced by the gene complex of the *fowleri* parent is the shape of the parotoid gland.

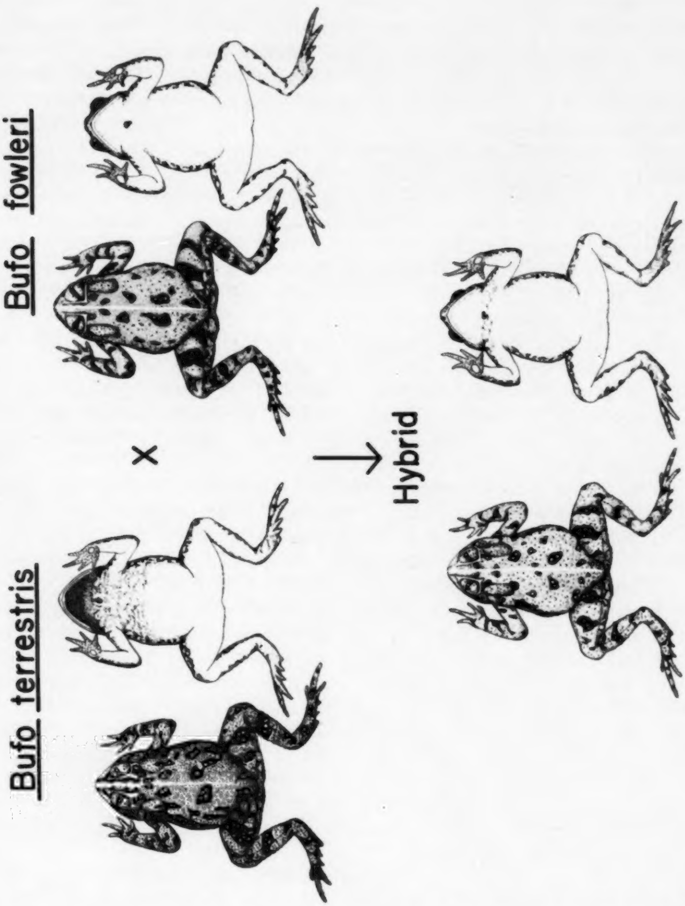

Fig. 2.—External features of the parents of the experimental cross, *B. terrestris* (Florida) X *B. fowleri* (New York), and of an F_1 hybrid derived from this cross.

EXPERIMENTAL SET II

B. terrestris ♀ (Slidell, La.)	X *B. terrestris* ♂ (Slidell, La.)
	X *B. fowleri* ♂ (Talisheek, La.)
B. fowleri ♀ (Talisheek, La.)	X *B. fowleri* ♂ (Talisheek, La.)
	X *B. terrestris* ♂ (Slidell, La.)

This experiment had a twofold purpose: first, to compare the F_1 hybrids between *terrestris* and *fowleri* individuals from Louisiana populations with the F_1 hybrids that resulted from the cross, *terrestris* (Florida) X *fowleri* (New York); and secondly, to compare the experimental F_1 hybrids with suspected natural hybrids collected in Louisiana populations.

The *terrestris* adults utilized in the crossing experiments were collected from a breeding congregation of the species at Slidell, Louisiana. The mating call of the males, a high-pitched trill, served to reinforce the impression derived from morphological examination that the breeding chorus consisted only of *terrestris* individuals. The *fowleri* adults were obtained at Talisheek, Louisiana, from a breeding congress made up only of this species, as judged by the drone-like mating calls and external features of the individuals.

The viability of the F_1 hybrids was normal. The cranial crests of the reciprocal F_1 hybrids compared favorably with those of hybrids derived from the cross, *terrestris* (Florida) X *fowleri* (New York). This similarity of the F_1 hybrids provided indirect evidence that the parental forms used in the experiments were essentially "good" representatives of each species.

The young hybrids resembled in miniature form several specimens of a suspected hybrid population collected at Pearl River, Louisiana. It may be inferred that the intermediate specimens found at Pearl River owe their origin to interspecific crosses. The Pearl River hybrid population will be considered in detail later.

Several aspects of the experimental crosses merit further consideration. As illustrated in Figure 2, the dorsal spots of *fowleri* individuals from the eastern seaboard tend to be arranged in pairs, each spot containing several small, rounded warts. In *fowleri* individuals from eastern Louisiana, the dorsal spots are less regularly disposed. Moreover, the warts tend to be larger and possess horny excrescences. Hence, where it may be possible to detect segregation in the size and nature of warts in a hybrid between an eastern coast *fowleri* and *terrestris,* the structural differences in warts between a Louisiana *fowleri* and *terrestris* are of such small magnitude that little or no segregation is discernible in the F_1 hybrid.

The venters of *fowleri* individuals from the Atlantic coast are typically immaculate, with or without median pectoral spots. In contrast, various degrees of ventral spotting may be found in Louisiana *fowleri* individuals from apparent "pure" populations. Several offspring from the Louisiana *fowleri* ♀ X *fowleri* ♂ cross possessed

spots on the ventral surface, a condition not encountered among the offspring of the New York *fowleri* ♀ X *fowleri* ♂ cross.

B. terrestris from Louisiana differs from its Florida counterpart with respect to the maximum size of the knob-like swellings on the posterior ends of the interorbital crests. These knobs in Louisiana adults do not attain the prominent size found among Florida individuals. The sizes illustrated by the lowermost pairs of toads (identifiable by numeral "4") in Figure 5 are characteristic of Louisiana *terrestris* adults. Similarly, the interorbital swellings were smaller in the offspring from the Louisiana *terrestris* X *terrestris* cross than in those from the Florida *terrestris* X *terrestris* cross.

EXPERIMENTAL SET III

B. terrestris-fowleri intermediate ♀ (Pearl River, La.)
X *B. terrestris-fowleri* intermediate ♂ (Pearl River, La.)

This cross involved two intermediate individuals collected near Pearl River, Louisiana that resembled the experimental F_1 hybrids. The two intermediate adults employed in the cross are illustrated in Figure 5 (pair of toads identifiable by numeral "2"). Populations near Pearl River (5-11 miles north of the town on Highway 41) appear on morphological grounds to be hybrid populations. The offspring of this cross constitute essentially an F_2 generation; the goal was to obtain as many recombination-type offspring as possible.

Thirteen hybrids from this cross were reared successfully beyond metamorphosis. When compared to each parental species, the individuals show various degrees of recombination of traits. The ventral surface is spotted in all offspring, ranging from a few markings in the pectoral region to numerous spots on the upper surface of the abdomen. The unspotted venter of *fowleri* and the heavy mottling of extreme members of *terrestris* were not recovered. This is not exceptional, since if it is assumed that ventral spotting is governed by a large number of polygenes, then the chances of recovering the extreme parental conditions are small.

The cranial crests tend toward the configuration of the experimental F_1 hybrids rather than that of either parental species. All offspring exhibit traces of a posterior extension of the interorbitals, but the projections are not knob-like. The largest-sized terminal prominence found among the offspring is comparable to that illustrated by the toad to the left of numeral "3" in Figure 5. Preparotoid connectives of variable lengths are present. Five of the progeny possess short preparotoid ridges, similar to those encountered in adult individuals (Fig. 5, pair of toads identifiable by numeral "1") in the hybrid population at Pearl River. The other eight offspring exhibit relatively long connectives, comparable to the ridges displayed by the pair of toads (numeral "2") in Figure 5.

No consistent pattern of arrangement of dorsal spots is evident,

nor can the sizes of the warts be characterized objectively. The warts range from small and round to large and spinous.

CHARACTER ANALYSIS OF NATURAL POPULATIONS

The data from the experimental crosses provided the necessary information as to the morphological characteristics that could be employed as indices of hybridization. Only two characters may be used. In Figure 3, the variations in shape of the cranial crests and the extent of ventral spotting have been broken up into five classes for each character. An individual may be symbolized by two index values, i.e., a separate score for each character. A rough estimate of variability in natural populations and some indication as to whether the variation is interspecific or intraspecific can be derived by an analysis of bar diagrams based on character index values (Fig. 4).

With respect to the cranial crests, a population containing a high frequency of individuals with index values of "4" would represent a *B. terrestris* population. The majority of individuals in a *B. fowleri* population would have index values of "0" for this character. In any population, individuals with intermediate values would be judged as intraspecific variants or interspecific hybrids on the basis of the relative frequencies in the population. A population containing a large proportion of individuals scoring "1," "2," and "3" would represent a hybrid population, particularly if some of the individuals resembled the experimental hybrids.

The extent of ventral spotting is a less reliable index of hybridization. The amount of ventral spotting ranges from "0" to "4" in *terrestris* populations. *B. fowleri* individuals are typically unmarked (index value "0"). However, individuals with values of "1," "2," and "3" may be found in apparently "pure" *fowleri* populations in Louisi-

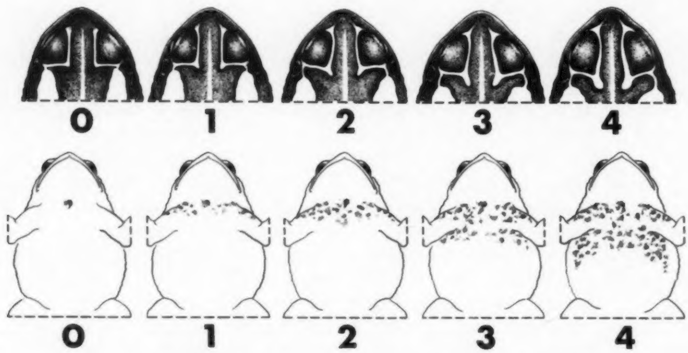

Fig. 3.—Range of variations ("0" to "4") in shapes of the cranial crests and the degree of ventral spotting.

ana. Thus, the presence of ventral markings in a *fowleri* individual does not necessarily indicate hybrid influences from *terrestris*. Nevertheless, *fowleri* populations in which occur a large number of individuals scoring "1," "2," and "3" as well as "4" would be suspected of having been modified by *terrestris*.

Certain limitations in the application of the "hybrid index" method are evident. Continuous variation cannot be precisely expressed in terms of five discrete classes. Individuals occur that bridge the gap

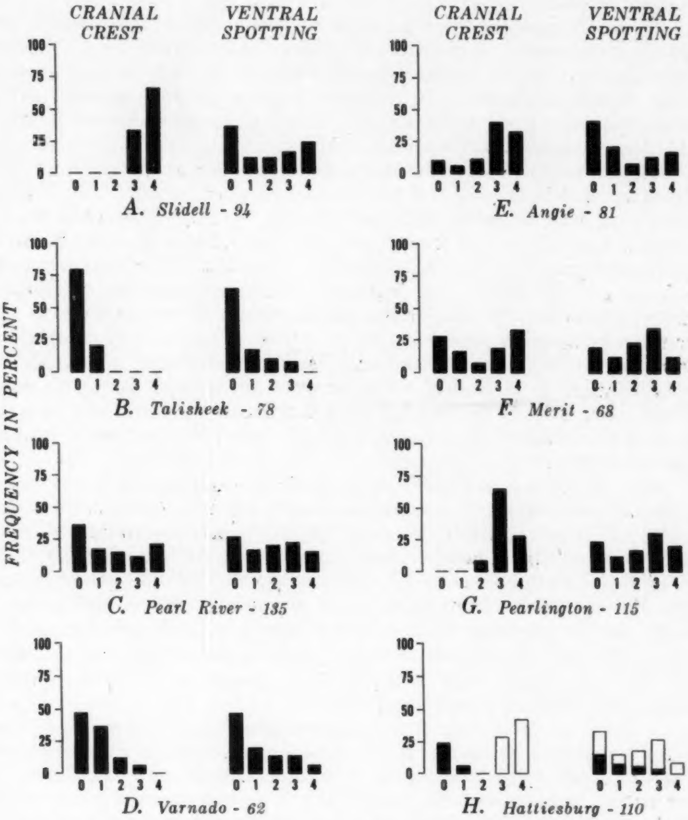

Fig. 4.—Frequency histograms of index values for two characters treated separately (cranial crests and ventral spotting) of eight populations. See text and Fig. 3 for meaning of index values. The locations of populations A-G are shown in Fig. 1. The numeral after the name of the locality represents the number of individuals plotted.

between any two of the five classes. Moreover, the assignment of an individual to a given class may be biased by the prior knowledge that the two species do or do not coexist in the particular population scored. Much of the bias was eliminated by rescoring each series several times at different occasions. The bar diagrams could be reproduced consistently and with sufficient accuracy to demonstrate the presence or absence of natural hybridization and to deduce the extent of interspecific gene exchange. In essence, the "hybrid index" method provides a rough, satisfactory measure of the effects of hybridization in natural populations.

Toads from eight large populations in southeastern Louisiana and adjacent Mississippi have been scored for each character. The percent distribution of character index values is represented in Figure 4. Two of the populations (A, B) represent relatively uniform samples of each species; the other six (C-H) illustrate the diverse ways in which the two species interact with each other.

Only *terrestris* individuals have been observed at Slidell, Louisiana (locality "A" in Figs. 1 and 4) over a two year period (1956, 1957). Three samples taken at different intervals during 1956 (March 25, April 2 and 15) and two collected in 1957 (May 13 and 25) were grouped together in preparing the bar diagrams. The *terrestris* individuals are typical of those found in southeastern Louisiana. Thirty-three percent scored "3" for the cranial crests. These individuals are considered as intraspecific variants. There is no indication that the terminal knobs of the interorbitals have been reduced as a result of hybridization with *fowleri.* The amount of ventral spotting ranges from index values "0" to "4," with the greater percent of the individuals possessing only a single pectoral spot ("0") or being heavily mottled ("4").

The population at Talisheek, Louisiana (locality "B") represents a *fowleri* assemblage. I am grateful to Mr. Paul K. Anderson for calling my attention to this apparently "pure" *fowleri* population. Collections on which the analysis is based were made on April 2, 15, and 23 of 1956. The cranial crests fall under categories "0" (80 percent) and "1" (20 percent). Most individuals are unmarked ventrally, but a small percent contain spots ranging from pectoral spotting (index value "1," 17 percent) to anterior abdominal spotting (index value "3," eight percent). Apparently spotting genes are present in uncontaminated stocks of *fowleri* in Louisiana.

A large array of character combinations was found in the Pearl River population (locality "C"). Samples were obtained on the evenings of April 4, 15, and 23 of 1956, and May 25 of 1957. Only 21 percent of the individuals possess the elevated knobs (index value "4") characteristic of *terrestris;* 36 percent exhibit the low, parallel crests of *fowleri* (index value "0"). These two extremes are connected by individuals with cranial values "1," "2," and "3." Fifteen percent of the individuals (index value "2") resemble the experimental F_1 hybrids. Two of these were used as parents in the laboratory crosses

reported above (Experimental Set III). Some of those that scored "1" and "3" are intraspecific variants; others are interspecific recombination types or backcross products. In other words, since types "1" and "3" may be found in "pure' aggregations of *fowleri* and *terrestris* respectively, it is difficult in a mixed population to distinguish an extreme variant within the species from an individual possessing some hybrid influences. Seventy-four percent of the individuals possess some degree of ventral spotting (values "1" - "4"), with four classes of spotting being fairly equally distributed. This suggests that *terrestris* spotting genes have infiltrated into the *fowleri* segment of the population.

The largest Pearl River sample (56 individuals) was obtained on the evening of April 23. The hybrid composition of the population is vividly demonstrated by a photograph of ten of the individuals collected on that evening (Fig. 5). The ten individuals are arranged in pairs, beginning with typical Louisiana *fowleri* (top pair, index value "0") and terminating with characteristic *terrestris* individuals (bottom pair, index value "4"). Figure 5 serves not only to illustrate photographically the continuous array of individuals that may be found in a hybrid population, but also the variation that may be expected within each class of index values. Figure 5 thus supplements the diagrammatic representation of the cranial crests (Fig. 3).

The individuals of the Varnado population (locality "D") are predominantly *fowleri*-like, but the variations in cranial crests and ventral spotting are greater than those found in the *fowleri* population at Talisheek. Individuals are present with cranial values "2" (11 percent) and "3" (6 percent), as well as individuals with reticulated venters (spotting value "4," 6 percent). It is believed that the greater variability has resulted from past hybridization with *terrestris* and repeated backcrossing to the *fowleri* component.

The result of continual backcrossing or introgression has also imparted greater variability to the population at Angie (locality "E"), but in this case the backcrossing has occurred to the *terrestris* stock. The present analysis of the Angie population is based on collections made by the Tulane field crew on June 2-6, 1950, and reported by Anderson, Liner, and Etheridge (1952). Although no detailed character analysis was made, these authors recognized that hybridization had taken place and recorded some of the individuals as "*Bufo terrestris/fowleri* intermediates." They also noted that *terrestris* was present in greater numbers than *fowleri*. It is of interest that, with respect to the cranial crests, more individuals (40 percent) are *terrestris*-like (crest value "3") than typically *terrestris* (crest value "4"). The data indicate that hybrid individuals have mated more often with the more abundant parental form (*terrestris*) than among themselves.

The three populations in Mississippi are quite different from each other in make-up. The Merit (locality "F") collection was derived from a mixed breeding congress that emerged on April 25, 1958. A

Fig. 5.—Composition of a hybrid population from Pearl River, Louisiana. The individuals are arranged in pairs and numbered according to index values represented in Fig. 3. *B. fowleri* individuals are represented by the top pair (index value "0"); F_1 hybrids by the middle pair ("2"); and *B. terrestris* by the bottom pair ("4"). The pairs with values "1" and "3" are intergrades between the F_1 hybrids and the respective species.

random sample of 68 individuals was taken by Dr. Royal D. Suttkus and Miss Myrna Andersson. They heard calls characteristic of each species as well as calls not referable to either species and thus presumably of hybrid individuals. The bar diagram indicates that hybridization has occurred, but gene exchange does not appear to have progressed as far as in the Pearl River population. The sample from Pearlington (locality "G") was also collected by Dr. Suttkus and Miss Andersson. The population is *terrestris*-like, with some indication of past hybrid influences from *fowleri*. An interesting feature of the population is the high number of individuals (64 percent) with reduced interorbital knobs (crest value "3"). The presence of some individuals (9 percent) with crest value "2" suggests that the interorbital prominences had been modified by *fowleri*.

The last series of individuals from Mississippi was collected by Mr. Benjamin E. Gandy from a locality ("H") six miles north of Hattiesburg on June 11, 1951. His field notes read: "Great numbers of *Bufo terrestris* and a few *Bufo fowleri* are calling in every roadside ditch and pond. Most of the *Bufo terrestris* are found around ponds and ditches in cultivated fields, but most of the *Bufo fowleri* are along the sandbars of the (Bowie) river." As revealed by the bar diagrams (Fig. 4), there is no indication that interbreeding has occurred. Individuals with cranial crest values "0" and "1" represent the *fowleri* segment of the population; those with values "3" and "4" comprise the *terrestris* portion. Since the two species are readily distinguishable from each other in this population, the frequency distributions of cranial crest and ventral spotting values are shown separately (darkened portions of bars pertain to *fowleri;* remaining light areas, *terrestris*). As in the "pure" *fowleri* population from Talisheek, different degrees of ventral spotting ("0" to "3") occur in the *fowleri* segment of the Hattiesburg population.

DISCUSSION

The occurrence of hybridization between *Bufo fowleri* and *Bufo terrestris* in the area of distributional overlap in southeastern Louisiana and adjacent Mississippi has been established by field observations, breeding tests, and character analyses of population samples. Individuals of each species may be found breeding side by side in the same pond. The gene complexes of the two species are interchangeable, resulting in viable hybrids. Experimental F_1 hybrids resemble some of the intermediate individuals collected in the field. Offspring derived from a cross of two natural hybrids exhibit a wide range of character recombinations. A comparable large variation in morphological characters has been found in population samples from the area of overlap of the two species. The case for natural hybridization appears well established.

Two prominent morphological characters, the shape of the cranial crests and the amount of ventral spotting, both of which are common-

ly employed to distinguish the two species, are easily modified by hybridization. Intraspecific variation in each of the characters, in the direction of the other species, is commonly encountered in Louisiana populations. In many populations, backcross individuals are difficult to distinguish from intraspecific variants. It is suspected, however, that introgression (extensive backcrossing to one of the parental species) has occurred in some of the populations.

B. fowleri individuals west of the area of contemporary contact with *B. terrestris* (i.e., in western Louisiana) exhibit *terrestris*-like characteristics. Many individuals from western Louisiana have prominent cranial crests (some with preparotoid ridges), spinous warts, and varied degrees of ventral spotting. Indeed, highly variable *B. fowleri* populations, apparently showing *terrestris*-like characteristics, may be found in most localities throughout Louisiana and eastern Texas.

It may be supposed that hybrid individuals from the area of overlap of the two species had migrated westward and have exchanged genes with the *B. fowleri* component, thus imparting greater variability to the *fowleri* stock in these areas. This would not explain the absence of *B. terrestris* in these localities, unless it is further assumed that *B. terrestris* had also migrated, but that the *terrestris* characteristics have been largely absorbed by extensive backcrossing to the more abundant *fowleri* individuals.

A more plausible explanation is that the *B. fowleri* populations in the western part of Louisiana were modified through past hybridization with an ancestral *terrestris*-like stock that differentiated into the *B. terrestris* group now occupying the southeastern part of the United States. In other words, the prototype of *B. terrestris* left its mark on the *B. fowleri* populations. The hybridization that is now occurring in the area of overlap of the two species is simply reinforcing the effects of extensive ancient hybridization.

What is the significance of the contemporary hybridization between *B. fowleri* and *B. terrestris* in the area of overlap? The main consequence has been to increase the variability of the two species. Greater variability has resulted from interspecific recombinations than could be realized from intraspecific crosses. The genetic spectrum has been expanded, providing a diversity of types upon which selection can operate. It is possible that new adaptive peaks may be realized from hybrid combinations. Some of the interspecific recombination products may be better adapted in certain habitats than the parental types. The very existence of natural hybrids does indicate that they must possess certain attributes that enable them to survive in nature. Or, if the hybrid individuals have the same adaptive values as the parental types, and are produced in considerable numbers, the hybrid individuals may bridge the gap between the two entities, resulting in a single highly variable assemblage. At present, the only obvious conclusion is that hybridization has modified and amplified the variation patterns of *B. terrestris* and *B. fowleri*.

SUMMARY

The occurrence of hybridization between *Bufo fowleri* and *Bufo terrestris* in the area of distributional overlap in southeastern Louisiana and adjacent Mississippi has been established by field observations, breeding tests, and character analyses of populations. The morphological characters distinguishing the two species are readily modified by hybridization. Notable modifications occur in the cranial crest components. The unique club-shaped, terminal prominences of the interorbital crests of *B. terrestris* are reduced to short, inwardly-curved, slightly raised projections in experimental F_1 hybrids. The latter also possess pronounced ridges (typically absent in *B. fowleri*) connecting the postorbital crests with the parotoid glands. Experimental F_1 hybrids resemble some of the individuals collected in mixed breeding aggregations of the two species. Offspring derived from a cross of two suspected natural F_1 hybrids are morphologically highly variable. Some hybrid populations exhibit a wide diversity of character recombinations ("hybrid swarms"); others apparently represent the outcome of repeated backcrossing of hybrids to one or the other parental species. In essence, the genetic spectrum has been expanded; greater variation has resulted from interspecific crosses than could be realized from intraspecific crosses.

REFERENCES

ANDERSON, E. 1936—Hybridization in American tradescantias. Ann. Missouri Bot. Gard. **23**:511-525.

———1949—Introgressive hybridization. John Wiley and Sons, Inc., New York.

ANDERSON, P. K., E. A. LINER, AND R. E. ETHERIDGE 1952—Notes on amphibian and reptile populations in a Louisiana pineland area. Ecology **33**:274-278.

BLAIR, A. P. 1941—Variation, isolating mechanisms, and hybridization in certain toads. Genetics **26**:398-417.

———1942—Isolating mechanisms in a complex of four species of toads. Biol. Symp. **6**:235-249.

———1947—Variation of two characters in *Bufo fowleri* and *Bufo americanus*. Amer. Mus. Nov. **1343**:1-5.

BRAGG, A. N. 1955—Taxonomic and physiological factors in the embryonic development of certain toads. Copeia **1955**:62.

——— AND O. SANDERS 1951—A new subspecies of the *Bufo woodhousii* group of toads (Salientia: Bufonidae). Wasmann Jour. Biol. **9**:363-378.

HUBBS, C. L. AND LAURA C. HUBBS 1943—Hybridization in nature between species of catostomid fishes. Contribs. Lab. Vert. Biol. **22**:1-76.

POLLISTER, A. W. AND J. A. MOORE 1937—Tables for the normal development of *Rana sylvatica*. Anat. Rec. **68**:489-496.

VOLPE, E. P. 1953—Embryonic temperature adaptations and relationships in toads. Physiol. Zool. **26**:344-354.

———1954—Hybrid inviability between *Rana pipiens* from Wisconsin and Mexico. Tulane Stud. Zool. **1**:111-123.

———1956—Experimental F_1 hybrids between *Bufo valliceps* and *Bufo fowleri.* Tulane Stud. Zool. **4**:61-75.

———1957a—Embryonic temperature tolerance and rate of development in *Bufo valliceps.* Physiol. Zool. **30**:164-176.

———1957b—Genetic aspects of anuran populations. Amer. Nat. **91**:355-372.

New Termites from Venezuela, with Keys and a List of the Described Venezuelan Species

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Early in 1956 Dr. Francisco Fernández-Yépez of the Universidad Central de Venezuela, Facultad de Agricultura, Maracay, Estado Aragua, kindly sent me a collection of eight species of termites. These were collected in various Venezuelan states from 1949 to 1955, mostly by him. Among them were two undescribed species.

In June, 1956, Dr. Fernández-Yépez sent an additional 13 species of termites, 7 of which he collected on a trip in the spring of 1956 to Venezuelan Guiana, Mt. Auyantepui, and 6 species from North Central Venezuela. Mt. Auyantepui is the site of Sir Arthur Conan Doyle's science-fiction, "The Lost World," an isolated, raised plateau on which (elsewhere) extinct prehistoric monsters still survived (1912). One new species was found in the material from Mt. Auyantepui.

I visited Venezuela in November and December, 1955 and found that *Heterotermes* damaged growing sugar cane, *Nasutitermes* cacao trees. *Heterotermes* and *Nasutitermes* were also the subterranean termites most injurious to buildings and material stored in them, while *Cryptotermes* was the dry-wood termite causing most damage to wooden furniture and the woodwork of buildings. Species of *Syntermes* harvest grass in the daytime; nests are underground. No soldier occurs in *Anoplotermes,* species of which may damage the roots of crops.

The discovery of the above-mentioned three new species brings the total number of termite species so far recorded from Venezuela to twenty-eight. A list and key to the known forms are appended below. Doubtless many other species occur in this large country with its varied climate.

Description of New Species

FAMILY KALOTERMITIDAE

Neotermes araguaensis, n. sp.

Winged female adult.—Head castaneous-brown, shining, longer than broad, slight depression and slope to front at epicranial suture, with scattered long hairs. Eyes black, large, not round, separated from lateral margin of head by a distance equal to their diameter and from posterior margin by a distance equal to twice their diameter. Ocelli large, projecting, at angle but close to eyes.

Labrum light castaneous brown, with short hairs.

Antennae pale yellow-brown, 19 segments, third and fourth short, ring-like, pubescent.

Pronotum light castaneous-brown, wider than head, twice as wide as long, roundedly emarginate anteriorly, very slightly posteriorly, sides rounded, with scattered short and long hairs.

Legs light, pale yellow-brown, tibiae yellow-brown, pulvillus between claws, not prominent.

Wings yellowish, veins yellow-brown, pubescent, median vein close to subcosta, extends to apex; in anterior wing subcostal vein with 8 (mostly long) branches to costa; cubitus nearer to subcosta than to lower margin of wing, with 11 branches to lower margin. Wing scale 1.6 in length.

Abdominal tergites light castaneous-brown, scattered long and short hairs.

Measurements:

Length of entire winged female adult	20.5 mm
Length of entire dealated female adult	10.5
Length of head (to tip of labrum)	2.4
Length of pronotum (where longest)	1.3
Length of hind tibia	1.9
Length of anterior wing	17.0
Diameter of eye (long diameter)	0.6
Width of head (at eyes)	2.2
Width of pronotum	2.75
Width of anterior wing	4.5

This species is larger than any of the 15 described Neotropical species of *Neotermes*.

Type locality.—Rancho Grande, Estado Aragua, Venezuela. Described from a series of winged adults collected at the type locality, 1100 m., 25-IV-'55 by F. Fernández-Yépez and C. J. Rosales. Other specimens collected at Km. 25, road Maracay-Choroni, Estado Aragua, 1500 m., 27-V-'55 by the same collectors and at the type locality on 14-VI-'55 by F. Fernández-Yépez alone. Also this species was collected at El Pilar, Estado Bolivar, 150 m., 21-VIII-'54 by F. Fernández-Yépez and C. J. Rosales, and at Guayaraca, Mt. Auyantepui, Estado Bolivar, 1020 m., 14-IV-'56 and 18-IV-'56 by F. Fernández-Yépez.

Holotype, winged female adult.—Cat. No. 63257, U. S. National Museum; *paratypes*, winged adults in U. S. National Museum and at Universidad Central de Venezuela, Maracay; *metatypes* and *topotypes* at these same institutions.

FAMILY TERMITIDAE

Anoplotermes franciscoi, n. sp.

Winged, female adult.—Head dark castaneous-brown, longer than broad, with dense long hairs. Fontanelle distinct, hyaline, subellipti-

cal slit on vertex of head. Post-clypeus yellow-brown, nearly three times as broad as long, bilobed, projecting, with long hairs.

Eyes black, nearly round, projecting, close to lateral margins of head. Ocellus hyaline, elliptical, projecting, at an angle to eye, separated from eye by a distance greater than the long diameter of the ocellus.

Mandible light yellow-brown, marginal teeth castaneous, elongate.

Antenna yellow-brown, 15 segments, third segment ring-like, shorter than second or fourth, pubescent.

Pronotum slightly lighter colored than head, saddle-shaped, with hyaline elliptical median marking and long hairs.

Meso- and meta-nota with posterior margins, roundly emarginate.

Wings smoky-gray, costal area yellowish, veins yellow-brown, punctate, pubescent. Anterior wing with median vein slightly above center of wing, closer to cubitus than to subcosta, reaches apex with four branches; cubitus does not reach apex, with 13 branches to lower margin of wing.

Measurements:

Length of entire winged female adult	19.5 mm
Length of entire winged male adult	18.0
Length of entire dealated female adult	10.0
Length of entire dealated male adult	9.0
Length of head (to tip of labrum)	2.4
Length of left mandible	1.1
Length of pronotum	1.0
Length of hind tibia	2.0
Length of anterior wing of female	16.5
Diameter of eye (long diameter)	0.37
Width of head (at eyes)	1.9
Width of pronotum	1.8
Width of anterior wing of female	4.0

This new *Anoplotermes* is larger than most of the 33 described neotropical species, it keys in close to the large species of Silvestri with fontanelle distinct and hyaline, but differs in size and morphological characters. I take pleasure in naming this species in honor of Dr. Francisco Fernández-Yépez of the Universidad Central de Venezuela.

Type locality.—Described from a series of winged adults collected at El Pilar, Estado Bolivar, approximately 150 m., 21-VIII-'54, by F. Fernández-Yépez and C. J. Rosales. Also this termite was collected at El Limon, cr. Maracay, Estado Aragua, 15-V-'56 by C. J. Rosales.

Holotype, winged female adult.—Cat. No. 63258, U. S. National Museum; *paratypes,* winged adults in U. S. National Museum and at Universidad Central de Venezuela, Maracay.

Velocitermes bolivari, n. sp.

Major Soldier.—Head dark castaneous-brown, nasus more reddish, broader than long, pear-shaped, slightly if any constricted anteriorly, two rows of bristles on dorsum of head, 4 bristles anteriorly, 2 poste-

riorly. Nasus conical short, with short hairs at tip. Mandible with conical point.

Antenna yellow-brown, with 14 segments, third slightly shorter than second or fourth, pubescent.

Pronotum slightly lighter colored than head, saddle-shaped, with row of long bristles on anterior margin and short hairs.

Legs yellow-brown, elongate, pubescent.

Abdominal tergites dark brown, a row of long bristles on posterior of each tergite, also dense shorter hairs.

Measurements:

Length of entire major soldier	5.25 mm
Length of head with nasus	1.75
Length of head without nasus (to anterior)	1.20
Length of nasus	0.55
Length of pronotum	0.25
Length of hind tibia	1.20
Width of head	1.20
Width of pronotum	0.75

Minor Soldier.—Head same color and shape as major soldier, bristles same, antennae same, in general smaller in size.

Measurements

Length of entire minor soldier	3.50 mm
Length of head with nasus	1.55
Length of head without nasus (to anterior)	1.0
Length of nasus	0.45
Length of pronotum	0.2
Length of hind tibia	0.9
Width of head	0.9
Width of pronotum	0.55

V. bolivari is distinct from the five other species of *Velocitermes* — all neotropical — in color, shape of head and relative size of third antennal segment. It is named in honor of Simón Bolivar, the South American liberator.

Winged, female adult.—Head dark castaneous-brown, lighter anteriorly, oval, longer than broad, with dense long and short hairs. Fontanelle a hyaline, narrow-Y-shaped slit.

Antenna yellow-brown, 17 segments, third shorter than second, slightly longer than fourth, pubescent.

Eye projecting, large, not quite round, rather close to lower margin head. Ocellus hyaline, suboval, prominent, at an angle to eye and at a distance from it equal to the short diameter of an ocellus.

Post-clypeus slightly lighter colored than head.

Pronotum light yellow-brown, posterior margin slightly roundedly emarginate, with dense long and short hairs.

Wings smoky, veins and costal area yellow-brown, surface punctate, margins densely hairy. Anterior wing with median vein with 4

branches to apex, closer to cubitus than to subcosta, above middle of wing; cubitus with 8 branches to lower margin wing at 5/7 of its length.

Abdominal tergites dark yellow-brown, darker than pronotum, with dense long and short hairs.

Measurements:

Length of entire female adult	15.5 mm
Length of entire female dealated adult	9.0
Length of head (to tip labrum)	1.70
Length of pronotum	0.75
Length of hind tibia	1.70
Length of anterior wing	12.0
Diameter of eye (long diam.)	0.4
Width of head	1.50
Width of pronotum	1.25
Width of anterior wing	3.5

This winged *Velocitermes* differs in size, color, the relative length of the third segment of the antenna and in wing venation from the other species whose winged adult has been described.

Type locality.—Guayaraca, Mt. Auyantepui, Estado Bolivar, 1020 m.

Described from a large series of major and minor soldiers collected with small and large (dimorphic) workers at the type locality, 18-IV-'56 by F. Fernández-Yépes.

Holotype, major soldier.—Cat. No. 63266, U. S. National Museum morphotype minor soldier. *Paratypes* and *morphotypes* in the U. S. National Museum and at the Universidad Central de Venezuela, Maracay.

Winged adults, 17 in number, collected at Uruyén (Gran Sabana), Estado Bolivar, 500 m., by F. Fernández-Yépez, 12-IV-'56 are either a new species of *Velocitermes,* or morphotypes of *V. bolivari* Snyder.

List of the Known Termites of Venezuela

FAMILY KALOTERMITIDAE

Kalotermes incisus Silvestri—Caracas.

Neotermes araguaensis, n. sp. Snyder—El Pilar, Guayaraca, Mt. Auyuantepui (Bolivar); Maracay — Choroni road, Rancho Grande (Aragua).

Cryptotermes brevis (Walker)—Caracas; Margarita Isld.

Glyptotermes latifrons (Silvestri)—La Trincheras (Carabobo).

G. pellucidus (Emerson).

Calcaritermes temnocephalus (Silvestri)—La Trincheras (Carabobo).

FAMILY RHINOTERMITIDAE

Heterotermes convexinotatus (Snyder)—Caracas, El Limón, cr. Maracay, Maracay (Aragua); Margarita Isld.

H. crinitus (Emerson)—Central Tacarigua (Carabobo); El Limón, cr. Maracay (Aragua).

Coptotermes testaceus (Linnaeus)—El Limón, cr. Maracay (Aragua); Puerto Cabello (Bolivar).

FAMILY TERMITIDAE

Anoplotermes franciscoi, n. sp. Snyder—El Limón, cr. Maracay (Aragua); El Pilar (Bolivar).

A. meridianus Emerson—El Limón, cr. Maracay, Rancho Grande, (Aragua).

A. subterraneus Emerson—El Limón (Aragua); Uruyén (Gran Sabana) (Bolivar).

A. tenebrosus (Kollar)—El Limón, cr. Maracay (Aragua).

Amitermes foreli Wasmann—Maracaibo (Zulia).

Microcerotermes arboreus Emerson—El Valle, D. F.

M. exiguus (Hagen)—El Valle, D. F.; El Limón, cr. Maracay (Aragua).

Syntermes grandis (Rambur)—Akuriman (Bolivar) upper Caroni River Basin.

S. molestus (Burmeister)—Akuriman, Ciudad Bolivar, Guayaraca, Mt. Auyantepui, Uruyén (Gran Sabana) Bolivar.

S. snyderi Emerson.

Nasutitermes corniger (Motschulsky)—Maracaibo, Zulia.

N. ephratae (Holmgren)—Guayaraca, Mt. Auyantepui, Uruyén (Bolivar); La Trincheras (Carabobo).

N. guayanae (Holmgren)—Uruyén (Bolivar); Valencia (Carabobo).

N. meinerti (Wasmann)—Kunana, Hoya del rio Negro, Perijá (Zulia); Moitaco (Bolivar).

N. nigriceps (Haldeman)—Acarigua (Portuguesa).

N. surinamensis (Holmgren).

Velocitermes bolivari, n. sp. Snyder—Guayaraca, Mt. Auyantepui, Uruyén (Bolivar).

Constrictotermes cavifrons (Holmgren).

Armitermes neotenicus Holmgren—Guayaraca, Mt. Auyantepui (Bolivar).

Total: 28 species.

KEY TO VENEZUELAN TERMITES

A. BASED ON WINGED FORMS

1. Fontanelle or head gland absent, forewing scale usually not much longer than pronotum, branches between costal and subcostal veins..................2.
   Fontanelle usually present, forewing scale longer than flat pronotum, no branches between costal veins..................4.
   Fontanelle usually present with plate, forewing scale shorter than saddle-shaped pronotum, no branches between costal veins..................6.

2. Median vein heavy, close to costal veins .... 3.
Median vein light, free from costal veins. *Kalotermes incisus* Silvestri.
Median vein light, usually united with subcostal vein near middle of wing .... *Cryptotermes brevis* (Walker).

3. Wing membrane stippled .... *Glyptotermes pellucidus* (Emerson).
Wing membrane stippled with brown spots .... *Calcaritermes*.
Wing membrane clear, large species .... *Neotermes araguanensis* Snyder.

4. Wing membrane punctate, wing margins ciliate, ocelli present or absent, fontanelle indistinct or absent, in middle of head .... 5.
Wing membrane reticulate, ocelli present, fontanelle in front or middle head .... *Coptotermes testaceus* (Linnaeus).

5. Wing membrane densely hairy; eye larger; length greater than 10.64 mm .... *Heterotermes crinitus* (Emerson).
Wing membrane with fewer hairs; eyes smaller, length 10.25 mm .... *Heterotermes convexinotatus* (Snyder).

6. Fore tibiae with two spines .... 7.
Fore tibiae with three spines (*Microcerotermes*) .... 13.

7. Left mandible with two nearly equal apical teeth; post-clypeus nearly twice as broad as long; antenna with 20-21 segments; fontanelle round; cubital vein does not reach apex of wing (*Syntermes*) .... 8.
First tooth left mandible longer than second; post-clypeus as long as its width; fontanelle round; antenna with 15 segments; pronotum not twice as broad as long; cubital vein does not reach apex of wing .... *Armitermes neoteinicus* Holmgren.
Fontanelle oval; antenna with 16 segments; pronotum twice as broad as long .... *Amitermes foreli* Wasmann.
Left mandible with two nearly equal apical teeth; post-clypeus shorter than half its width; fontanelle elongate, triangular, or Y-shaped; antenna with 15-17 segments; cubital vein reaches apex of wing .... 9.
Left mandible with first tooth much longer than second; post-clypeus shorter than half its width; fontanelle distinct; antenna with 15 segments, third segment very short; meso-and metanota notched; cubital vein does not reach apex of wing (*Anoplotermes*) .... 10.

8. Anterior corners of pronotum very pointed at tip; post-clypeus raised up .... *Syntermes snyderi* Emerson.
Anterior corners of pronotum nearly rectangular; post-clypeus fairly flat .... *Syntermes grandis* (Rambur).
Anterior corners pronotum strongly rounded; smaller, length 28 mm .... *Syntermes molestus* (Burmeister).

9. Third segment of antenna shorter than second .... *Velocitermes*.
Third segment of antenna longer than second .... *Constrictotermes cavifrons* (Holmgren).
Third segment of antenna shorter than second (*Nasutitermes*) .... 12.

10. Winged adults large, 14-19 mm in length .... 11.
Winged adults small 10.50 mm in length; ocelli less than their width distant from eyes; fontanelle white, same size as an ocellus .... *Anoplotermes subterraneus* Emerson.

11. Length 14.00 mm; fontanelle small, elongate.. *Anoplotermes meridianus* Emerson.
    Length 16.50 mm; fontanelle small, sub-oval.. *Anoplotermes tenebrosus* (Kollar).
    Length 19.50 mm; ocelli distant from eyes greater than their length; fontanelle hyaline, subelliptical slit........*Anoplotermes franciscoi* Snyder.

12. Antenna with 16 segments; ocelli distant about half their length from eyes; 17 m in length........................*Nasutitermes guayanae* (Holmgren).
    Antennae with 16 segments; ocelli very close to eyes; 14.50 mm in length..*Nasutitermes nigriceps* (Haldeman).
    Antenna with 15 segments; ocelli distant from eyes; 14 mm in length ....*Nasutitermes corniger* (Motschulsky).
    Ocelli slightly more than their diameter distant from eyes...................... ....*Nasutitermes surinamensis* (Holmgren).
    Ocelli close to eyes; 14.50 mm in length.. ....*Nasutitermes ephratae* (Holmgren).

13. Length 9 mm..*Microcerotermes arboreus* Emerson.
    Length shorter ....*Microcerotermes exiguus* (Hagen).

B. BASED ON SOLDIERS

1. Soldier absent; worker body fusiform; post-clypeus strongly arched; pronotum saddle-shaped; tibiae of forelegs swollen....................*Anoplotermes*.

2. Soldier present; no fontanelle or head gland; mandibles functional, used for biting, with marginal teeth; pronotum flat, broader than head........3.
   Fontanelle present; mandibles functional, used for biting, without marginal teeth; pronotum flat, narrower than head..................................6.
   Mandibles usually with marginal teeth, pronotum saddle-shaped............8.
   Fontanelle present; mandibles degenerate and non-functional, with or without points; head prolonged into a beak or nasus; pronotum saddle-shaped ....11.

3. Front of head steeply sloping anteriorly, lobed, blackish, length 2.4 mm; antenna with 13 segments........................*Glyptotermes latifrons* (Silvestri).
   Head dark red, length 1.6 mm; antenna with 11-12 segments; apical spur on fore tibia........................*Calcaritermes temnocephalus* (Silvestri).

4. Head profile concave, roughened anteriorly, black, length 1.88 mm; antenna with 13 segments........................*Cryptotermes brevis* (Walker).

5. Front of head not steeply sloping, lobed or concave; third segment antenna greatly modified, longer than second or fourth; hind femora swollen ....*Kalotermes incisus* Silvestri.
   Third segment antenna not modified; hind femora slender........*Neotermes*.

6. Head elongated, parallel-sided; fontanelle without tubular elongation; labrum pointed at tip; mandibles nearly straight......................................7.
   Head narrowed anteriorly; fontanelle opening at front with short tube; mandibles bowed..................................*Coptotermes testaceus* (Linnaeus).

7. Head covered with hairs............................*Heterotermes crinitus* (Emerson).
   Head with very few hairs................*Heterotermes convexinotatus* (Snyder).

8. Mandibles bowed, tip curved inwards, single, central marginal tooth on each .... *Amitermes foreli* Wasmann.
   Central or basal tooth on mandibles; prothorax with lateral spines or projections .... 9.
   Basal tooth on each mandible; head with elongate nasus........ *Armitermes neoteinicus* Holmgren.
   Mandibles elongate with minute serrations; antenna with 13 segments....10.

9. Width of head 6.81 mm; marginal teeth prominent; notal spines elongate .... *Syntermes snyderi* Emerson.
   Width of head 5.93 mm .... *Syntermes grandis* (Rambur).
   Width of head 2.87 mm; marginal teeth not prominent; no notal spines .... *Snytermes molestus* (Burmeister).

10. Length of head 2.67 - 2.73 mm........ *Microcerotermes arboreus* Emerson.
    Head shorter .... *Microcerotermes exiguus* (Hagen).

11. Head not depressed, dorsal profile convex; antenna with 13-14 segments .... 12.
    Head depressed, dorsal profile concave; one type of soldier, antenna with 15 segments, third nearly double length of second........ *Constrictotermes cavifrons* (Holmgren).
    Two types of soldiers; antenna with 17 segments, third shorter than second or fourth........ *Velocitermes bolivari* Snyder.

12. Head length 1.4 - 1:60 mm, reddish-brown, with few hairs; nasus long, cone-shaped; antenna with 13 segments, third longer than second; tergites with microscopic hairs........ *Nasutitermes corniger* (Motschulsky).
    Head dark reddish-brown; tergites without microscopic hairs........ *Nasutitermes ephratae* (Holmgren).
    Head length 1.75 - 1.80 mm, dark brown, with few hairs; nasus long, cone-shaped; antenna with 14 segments, third as long as second; tergites without microscopic hairs........ *Nasutitermes guayanae* (Holmgren).
    Head reddish-brown; nasus long and thick, cylindrical; antenna with 13 segments, third longer than second........ *Nasutitermes surinamensis* (Holmgren).
    Head brown; nasus short, relatively small, nearly cylindrical; antenna with 13 segments, third longer than second; tergites with microscopic hairs .... *Nasutitermes meinerti* (Wasmann).
    Head length 1.75 - 1.90 mm, blackish brown, densely hairy; nasus short, cone-shaped; antenna with 13 segments, third almost double length of second; tergites with hairs........ *Nasutitermes nigriceps* (Haldeman).

Resumen

Nuevos Comejenes (Isoptera) de Venezuela.—El autor revisa los Isoptera de Venezuela, basado en parte en el material de la Facultad de Agronomía de la Universidad Central, llegando a un total de 28 especies. De ellas, tres son descritas como nuevas para la ciencia: *Neotermes araguaensis, Anoplotermes franciscoi* y *Velocitermes bolivari.* Claves para las formas aladas y soldados de las especies venezolanas son incluídas en el trabajo.

Algae in Colorado Soils

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The algae are important constituents of the living, changing complex that we call the soil. Soil contains not only minute mineral fragments but also water, gases, dead plant materials, insect larvae, nematodes, protozoa, bacteria, fungi and algae. This is an intricate association and the algae have a part in it. They add organic matter to the soil, influence chemical changes therein, are known to fix nitrogen and are a food source for small animal life in the soil.

Several workers throughout the world have listed the various algae they have found in the soil (Bristol-Roach, 1927; Fritsch, 1922; Fritsch and Salisbury, 1915; Russell, 1923) and a few have studied the activities of these micro-organisms (Bristol, 1920; Petersen, 1935; Skinner, 1932). Most of these studies were made in Europe. In this country as early as 1912, W. W. Robbins examined 22 soils and found 12 species of algae living in them. Later, G. T. Moore and associates (1919; 1926) listed 31 species of algae found existing in soils at the Missouri Botanical Gardens, some of them rather deep below the surface. In 1925, Bonar and Goldsmith made a study of desert soils in the Southwest and found that such soils contained a total of 14 genera of algae; no specific list was published. Lowe and Moyse (1934) listed 27 species of algae from soils of Manitoba, Canada.

The limited information on soil algae in this country suggests a need for further inventory, especially in the intermountain West. It is the purpose of the following paper to list such algae as have been found in Colorado soils, with brief mention of the conditions of their habitat.

Methods

Soil samples were collected with a sterilized trowel and placed in sterile soil cans. All samples were taken from the top four inches of soil except for a few that were taken from cut banks at some depth below the surface. Before digging, the top half inch or so of soil was scraped away. In the case of lateral sampling in cut banks, the surface was removed to a depth of several inches to a foot, before the actual sample was taken.

In the laboratory the soil in most cases was tested for acidity with the aid of a Beckman pH meter. Approximately two grams of soil from each sample can were then put into a sterile 125 cc. Erlenmeyer flask. The bottom of the flask was covered with clean quartz sand. The cotton-plugged flasks, containing the sand and a nutrient solution (modified Bristol-Roach), had been autoclaved prior to inoculation with the soil samples. The mouths of the flasks were covered

with sheet paraffin over the cotton plugs and placed in racks facing a north window. The flasks were tipped at an angle so that the upper side of the quartz substrate was more or less drained. After 60 days, growth usually had occurred, and the cultures were examined and their components identified. Most of the cultures were re-examined after six months or more, since species frequently developed which were not found in the first examination. Judging from the way algae develop in these cultures, it appears that a two gram sample of soil may have only one to a few algal cells in its mass. Many flasks contained monoalgal cultures after standing several months.

RESULTS

Two hundred and twenty-three soils were sampled from various localities throughout the state, representing irrigated farm land, dry farm land, grassland, mountain and forest soil. From samples of these soils, 85 species of algae were identified, representing 40 genera. Of these, 21 genera were of green algae and 17 were blue-green forms. The following is a list of the species found:

PHYLUM CHLOROPHYTA

CLASS CHLOROPHYCEAE

Chlamydomonas angulosa Dill
Haematococcus lacustris (Girod.) Rostaf.
Pamella mucosa Kuetzing
Sphaerocystis Schroeteri Chodat
Gloeocystis ampla (Kuetz.) Lagerheim
Gloeocystis gigas (Kuetz.) Lagerheim
Gloeocystis planctonica (West & West) Lemmermann
Gloeocystis major Gerneck
Gloeocystis vesiculosa Naegeli
Palmogloea protuberans (Sm. & Sow.) Kuetzing
Dispora crucigenioides Printz
Stichococcus subtilis (Kuetz.) Klercker
Stichococcus bacillaris Naegeli
Stichococcus scopulinus Hazen
Protococcus viridis C. A. Agardh
Chlorococcum humicola (Naeg.) Rabenhorst
Characium Pringsheimii A. Braun
Pediastrum Boryanum (Turp.) Meneghini
Chlorella ellipsoidea Gerneck
Chlorella vulgaris Beyerinck
Trochiscia obtusa (Reinsch) Hansgirg
Trochiscia granulata (Reinsch) Hansgirg
Planktosphaeria gelatinosa G. M. Smith
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus convolutus Corda
Kirchneriella obesa (W. West) Schmidle
Kirchneriella lunaris (Kirch.) Moebius
Quadrigula Chodatii (Tan.-Ful.) G. M. Smith
Scenedesmus bijuga (Turp.) Lagerheim
Scenedesmus dimorphus (Turp.) Kuetzing
Mesotaenium Greyii Turner
Mesotaenium Endlicherianum Naegeli
Mesotaenium macrococcum (Kuetz.) Roy & Bliss
Cosmarium angulare Johnson

PHYLUM EUGLENOPHYTA

CLASS EUGLENOPHYCEAE

Euglena sp.

PHYLUM CHRYSOPHYTA

CLASS XANTHOPHYCEAE

Bumilleria exilis Klebs
Bumilleria sicula Borzi

PHYLUM CYANOPHYTA

CLASS MYXOPHYCEAE

Coccochloris aeruginosa Drouet & Daily
Coccochloris stagnina Sprengel
Anacystis montana f. *montana* Drouet & Daily
Anacystis montana f. *gelatinosa* Drouet & Daily
Anacystis dimidiata Drouet & Daily
Anacystis thermalis f. *major* (Lager.) Drouet & Daily
Spirulina major Kuetzing
Oscillatoria formosa Bory
Oscillatoria Haemelii Fremy
Oscillatoria curviceps C. A. Agardh
Oscillatoria limnetica Lemmermann
Oscillatoria Agardhii Gomont
Oscillatoria limosa (Roth) C. A. Agardh
Oscillatoria tenuis C. A. Agardh
Oscillatoria terebriformis C. A. Agardh
Phormidium tenue (Menegh.) Gomont
Phormidium ambiguum Gomont
Phormidium inundatum Kuetzing
Phormidium Retzii (C. A. Ag.) Gomont
Phormidium favosum (Bory) Gomont
Lyngbya major Meneghini
Lyngbya versicolor (Wartmann) Gomont
Lyngbya limnetica Lemmermann
Lyngbya aestuarii (Mert.) Liebmann
Lyngbya Martensiana Meneghini
Microcoleus lacustris (Rab.) Farlow
Microcoleus paludosus (Kuetz.) Gomont
Schizothrix Friesii Gomont
Schizothrix fasciculata (Naeg.) Gomont
Anabaena torulosa (Carm.) Lagerheim
Anabaena aequalis Borge
Anabaena oscillarioides Bory
Aulosira implexa Bornet & Flahault
Nostoc paludosum Kuetzing
Nostoc pruniforme C. A. Agardh
Nostoc caeruleum Lyngbye
Nostoc muscorum C. A. Agardh
Cylindrospermum punctatum Woronichin
Cylindrospermum majus Kuetzing
Cylindrospermum licheniforme (Bory) Kuetzing
Cylindrospermum muscicola Kuetzing
Nodularia Harveyana (Thw.) Thuret
Nodularia spumigena Mertens
Scytonema Archangelii Bornet & Flahault
Scytonema tolypothricoides Kuetzing
Fremyella Goeppertiana Kirchner
Stigonema turfaceum (Berkeley) Cooke
Calothrix fusca (Duetz.) Bornet & Flahault

Certain species occurred commonly: 120 samples contained *Chlorococcum humicola;* 89 contained species of *Phormidium;* 56 contained species of *Chlorella;* 50 samples bore *Protococcus viridis;* 42 had species of *Oscillatoria;* 38, species of *Stichococcus;* 34, species of *Nostoc;* and 24 bore species of *Gloeocystis*. The other species listed were con-

tained in one to a few samples of soil. Seven samples developed no algae. Moss protonemata were fairly common, some even occurring in the dry prairie soils.

It is of interest to note the presence of the various species of algae in the environments from which the soils were taken. Most of the soils sampled in this region were alkaline, although some of the mountain soils were acidic. Generally speaking, the blue-green algae were most prevalent in alkaline soils; this is in agreement with the statements of Lund (1946, 1947, and 1948) and others. In one lot of samples, ranging from pH 8.6 to 10, the following forms were present: *Phormidium tenue, P. Retzii, Nostoc paludosum, N. muscorum, Oscillatoria Agardhii, Nodularia spumigena, N. Harveyana,* three species of *Lyngbya, Schizothrix fasciculata, Microcoleus lacustris, Scytonema Archangelii* and *Fremyella Goeppertiana.*

In these same alkaline soils, several green algae occurred quite regularly: *Chlorococcum humicola, Protococcus viridis, Gloeocystis vesiculosa* and species of *Trochiscia.* In fact, *Chlorococcum humicola* is able to grow and survive at conditions from pH 4.2 to 10. Soil samples from white alkali spots contained *Chlorococcum humicola* and *Phormidium tenue. Fremyella Goeppertiana* and *Lyngbya major* occurred in soils having a pH of 9.3.

Certain forest soils under duff registered pH 9.5 and contained *Chlorococcum humicola, Chlorella vulgaris, Stichococcus subtilis* and *Mesotaenium Endlicherianum.*

Soils under salt grass from San Luis Valley with a pH of 9.5 to 10 contained *Chlorococcum humicola, Chlorella vulgaris, Protococcus viridis, Nostoc paludosum, Nodularia Harveyana, Lyngbya versicolor, Phormidum tenue.* A sample from salt grass-marsh pasture in northern Colorado contained only *Protococcus viridis* and *Phormidium tenue.*

Soils from greasewood flats with a pH of 9.5 contained *Phormidium tenue, P. Retzii, Nostoc paludosum, N. muscorum* and *Stigonema turfaceum.*

Samples from blow soil contained *Phormidium tenue, Anacystis montana* f. *montana, Oscillatoria formosa* and also moss protonemata.

Under sage brush (soil of pH 6.5) were found *Phormidium Retzii, Chlorococcum humicola, Chlorella vulgaris, Nostoc muscorum* and *Stichococcus subtilis.*

In 31 dryland soil samples from the eastern part of Colorado, 20 contained *Chlorococcum;* 17, *Phormidium* sp.; 16, *Protococcus;* 11, *Stichococcus;* 7, *Chlorella;* 7, *Nostoc;* 4, *Sphaerocystis;* 3, *Anacystis thermalis* f. *major;* 3, *Gloeocystis;* and one each contained *Cosmarium, Mesotaenium, Trochiscia, Dispora* and *Bumilleria.*

Under buffalo grass sod occurred species of *Nostoc, Schizothrix, Phormidium, Chlorococcum, Protococcus,* and *Stichococcus. Haema-*

tococcus lacustris and *Cosmarium angulare,* which probably blew in from elsewhere and lay dormant, also occurred.

From unirrigated grain fields, species of the following were found: *Cylindrospermum, Phormidium, Oscillatoria, Chlorococcum, Protococcus* and *Bumilleria.*

Alpine soils vary greatly in pH, from a low of 3.5 to a high of 9.5 to 10. A variety of algae occurred at high altitudes. From wet tundra at 12,000 feet altitude were isolated: *Oscillatoria limnetica, O. tenuis, Gloeocystis ampla, G. major, Chlorococcum humicola, Mesotaenium Endlicherianum, Quadrigula Chodatii;* from nearby dry tundra: *Chlorococcum humicola, Chlorella vulgaris, Oscillatoria limnetica, Mesotaenium Endlicherianum, Stichococcus subtilis* and *Coccochloris aeruginosa.* A few alpine soils of low pH apparently contained no algae.

Numerous samples were taken from lake and stream banks where the soil was wet or saturated, and a few samples were also taken from old, dried lake bottoms. These samples contained *Chlamydomonas angulosa, Sphaerocystis Schroeteri, Gloeocystis ampla* and *Oscillatoria Haemelii.*

Mud from a drained lake bed contained *Protococcus viridis, Lyngbya major, Fremyella Goeppertiana.*

Soil from an old, dried stream bed yielded *Nostoc muscorum, Phormidium tenue, P. Retzii, Spirulina major, Coccochloris aeruginosa, Protococcus viridis, Chlorococcum humicola* and *Lyngbya aestuarii.*

Mud near edge of pools developed *Phormidium tenue, P. Retzii, Chlorococcum humicola, Oscillatoria formosa, O. limnetica, O. Agardhii, Ankistrodesmus falcatus, Chlorella vulgaris, C. ellipsoidea, Anacystis thermalis* f. *major, Kirchneriella lunaris, Anacystis montana* f. *montana, Euglena* sp., *Stigonema turfaceum, Coccochloris aeruginosa, Nodularia Harveyana, Gloeocystis ampla, G. major* and *Mesotaenium Endlicherianum.* No doubt some of these species were washed or splashed there.

Several soil samples were taken from deep cut banks, care being taken to dig back a foot or so to avoid surface contamination. *Chlorella vulgaris* was found three feet from the surface in one instance; in another, *Chlorella vulgaris, Stichococcus subtilis* and *Chlorococcum humicola* were found at a depth of one foot. Some samplings were made from the surface to as deep as 15 feet. All of the deeper samples were free of algae. Hardpan occurred at about one foot from the surface and no doubt acted as a barrier.

Three successive seasonal samplings were taken from ten marked stations across a cultivated grass area. Little can be drawn from the results except that *Chlorococcum humicola* and *Phormidium tenue* were always present while a few other species occurred at random.

One set of samples from dry iron red soils, derived by disintegration of neighboring rock deposits, contained very few to no algae.

A collection of 35 soils from the dry plains, stored dry in bags for two years, yielded several algae:

21 of these samples developed	*Chlorococcum humicola*
17 " " " "	*Phormidium* species
9 " " " "	*Protococcus viridis*
8 " " " "	*Oscillatoria* species
10 " " " "	*Stichococcus bacillaris*
7 " " " "	*Chlorella vulgaris*
4 " " " "	*Gloeocystis* species
1 " " " "	*Trochiscia* species
5 " " " "	*Sphaerocystis Schroeteri*
1 " " " "	*Nostoc paludosum*

Two years is a short storage period; judging from other studies with stored soils, the above results would be expected. B. Muriel Bristol (1919) obtained over 30 species in stored soil samples. *Phormidium tenue* survived in these samples after 51 years storage, *Chlorococcum humicola* after 59, and *Nodularia Harveyana* after 71 years.

SUMMARY

The above study consists chiefly of an inventory of algae found in different soil localities in Colorado. Comparing the Colorado list with those of other observers in other countries, there is a great similarity of species found in soil. Certain species seem universal, others rare, or occurring by chance. From our knowledge of the size of these organisms, their tenacious hold on life, and the many ways they can be distributed, it is not surprising to find comparable lists of species over widely separated areas.

REFERENCES

BONAR, LEE AND G. W. GOLDSMITH 1925—Distribution and behavior of soil algae. Carnegie Inst. Year Book **24**:324.

BRISTOL, B. M. 1919—On the retention of vitality by algae from old stored soils. New Phytol. **18**:92-107.

———1920—On the algal flora of some desiccated English soils. Ann. Bot. **34**:35-81.

BRISTOL-ROACH, B. M. 1927—On the algae of some normal English soils. Jour. of Agric. Sci. **17**:563-588.

FRITSCH, F. E. 1922—The terrestrial algae. Jour. Ecology **10**:220.

——— AND E. J. SALISBURY 1915—Further observations on the heath associations on Hindhead Common. New Phytol. **14**:116-138.

LOWE, C. W., AND A. V. MOYSE 1934—An investigation of some Manitoba soils for presence of algae. Trans. Roy. Soc. Canada **28**:119-152.

LUND, J. W. G. 1946—Observations on soil algae. 1. New Phytol. **45**:56-110.

———1947—Observations on soil algae. 2. New Phytol. **46**:35-60.

———1948—Observations on soil algae. 3. New Phytol. **46**:185-194.

MOORE, G. T., AND JOAN L. KARRER 1919—A subterranean algal flora. Ann. Miss. Bot. Gard. **6**:281-307.

——— AND NELLIE CARTER 1926—Further studies on the subterranean algal flora of Missouri Botanical Garden. Ann. Miss. Bot. Gard. **13**:101-140.

PETERSEN, JOHS. BOYE 1935—Studies on the biology and taxonomy of soil algae. C. H. Reitzels Forlag, Kobenhavn. 183 pp.

ROBBINS, W. W. 1912—Algae in some Colorado soils. Colo. Agr. Exp. Stat. Bul. **184**:24-36.

RUSSELL, J. 1923—The microorganisms of the soil. Longmans, Green and Co., London. pp. 99-114.

SKINNER, C. E. 1932—Soil as a habitat for growth of green algae. Soil Sci. **34**:25-28.

Synopsis of Louisiana Polypores

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The objective of this paper is to make a survey of the polypores that have been reported from Louisiana to the present time. One of the first lists of Louisiana fungi was published by Featherman (1871, 1872) reporting some fifteen species. The most comprehensive list of Louisiana polypores published in the eighteen hundreds was that of the Rev. A. B. Langlois. His "Catalogue Provisoire" of 1887 was the result of eight years' collecting of phanerogams and cryptogams, mostly in the southern part of the state. Few published records of Louisiana polypores have appeared since that time. The most important studies that have come to our attention include the work of Murrill (1907), Lloyd (1912), Burt (1917), Overholts (1953), and Lowe (1957). Because it is desirable to have as complete a record as possible, all of the species not collected by us, but reported by the above authors, have been included. An annotated list of the collections we have studied is presented together with photographs of some of the more interesting species. The conservative nomenclature adopted by Overholts has been followed except for Ganoderma. Synonyms are given where recent investigations have shown that their omission might lead to confusion. Collections are reported by parishes; the following abbreviations are used: Ascension (A), East Baton Rouge (EBR), Evangeline (E), Grant (G), Iberia (I), Iberville (Iv), Jefferson (J), Livingston (L), Madison (M), Natchitoches (N), Orleans (O), Pointe Coupee (P), Rapides (R), St. Charles (St.C), St. Helena (St.H), St. John the Baptist (St.J), St. Landry (St.L), St. Martin (St.M), St. Tammany (St.T), Tangipahoa (T), Washington (W), Webster (Wb), West Baton Rouge (WBR), West Feliciana (WF). Collection numbers preceded by a "P" refer to Lowy's collections; Welden's numbers are prefixed, "ALW." A number of collections of both authors are unnumbered. To avoid confusion as many duplicates as possible have been deposited at Baton Rouge and at New Orleans.

Key to Genera of Louisiana Polyporaceae

1. Sporophore resupinate 2
1. Sporophore effuso-reflexed, sessile, to stipitate, not resupinate 4
    2. Pores shallow, sometimes represented only by folds or reticulations over which the hymenium is continuous; waxy to gelatinous hymenium .... *Merulius*
    2. Pores well-developed and sterile on their edges 3
3. Pores relatively large, sunken to unequal depths in context, often with a narrow free margin .... *Trametes*

3. Pores smaller, their bases forming a continuous line in the context, strictly resupinate .... *Poria*[1]
   4. Spores light to dark brown, truncate and appearing echinulate; pileus with a crust .... *Ganoderma*
   4. Spores not truncate or, if so, then not appearing echinulate; pileus with or without a crust 5
5. Pores very shallow in mature specimens, separated by narrow ridges or folds over which the hymenium is continuous; waxy or gelatinous hymenium .... *Merulius*
5. Pores deeper, well-developed, and sterile over their edges 6
   6. Sporophores perennial; tubes in several layers, especially hard and woody .... *Fomes*
   6. Sporophores annual or scarcely lasting two or three years; tubes generally not in distinct layers 7
7. Pore surface of radiating lamellae .... *Lenzites*
7. Pore surface various but not lamellate 8

[1] Not treated in this paper.

Fig. 1.—*Polyporus giganteus* Pers. ex Fr. Upper surface of sporophore. Scale shown.

8. Pores large and hexagonal 9
8. Pores smaller, angular, circular, sinuous (daedaloid), but not hexagonal 10
9. Sporophore sessile .... *Hexagona*
9. Sporophore stipitate; pores arranged in rows radiating outward from stipe .... *Favolus*
10. Pore surface sinuous .... *Daedalia*
10. Pore surface poroid or hydnoid; if hydnoid, traces of pores usually present along margin 11
11. Pore surface hydnoid 12
11. Pore surface poroid, edges of pores may be toothed but distinct pores present on hymenial surface 14
12. Context white .... *Polyporus tulipiferae*
12. Context brown 13
13. Setae present .... *Hydnochaete*[1]
13. Setae absent .... *Trametes*
14. Context not distinct from pore tissue; tubes often sunk to uneven depths .... *Trametes*
14. Context distinct from pore tissue; tubes not sunken to uneven depths in context but forming a continuous line .... *Polyporus*

DAEDALIA Pers. ex Fr.

Sporophores coriaceous to corky, never fleshy and soft; context white or light-colored; hymenium of elongated or sinuous pores, sometimes varying toward poroid or lamellate. Overholts reports five species from Louisiana. We have collected and studied two species, one of which has not previously been reported.

1. Pores or interspaces 1 mm or more broad, walls thick, obtuse; on hardwoods .... *D. quercina*
1. Pores 1-3 per mm, or interspaces less than 1 mm broad, walls thin rarely lamellate .... *D. ambigua*

1. *D. ambigua* Berk.—A very large specimen 58 x 25 cm (Fig. 12), was collected (4 VII 56) on an oak log in EBR. Although the dimensions are beyond the range indicated by Overholts for the species, there can be no doubt as to its identity.

Specimens: 5 X 55, EBR; 8 X 55, WBR; 5 V 56, St.T; 15 X 56, EBR; 125 P; 23 V 56, ALW 66, T; 30 V 56, EBR, 131 P; 4 VII 56, WF; 13 IV 57, L; 24 III 57, St.C, ALW 286.

2. *D. quercina* L. ex Fr.—This species appears to be unreported from this state. Its typical distribution is farther north.

Specimens: 5 VIII 52, EBR; 2 VII 56, WF.

FAVOLUS Beauv. emend. Fr.

Fructifications stipitate or substipitate with hexagonal pores arranged in rows radiating outward from the stipe.

1. Pores scarcely visible to the unaided eye, 3-4 per mm; sporophores rarely more than 2 cm diam. .... *F. Rhipidium*
1. Pores easily visible to the unaided eye 2

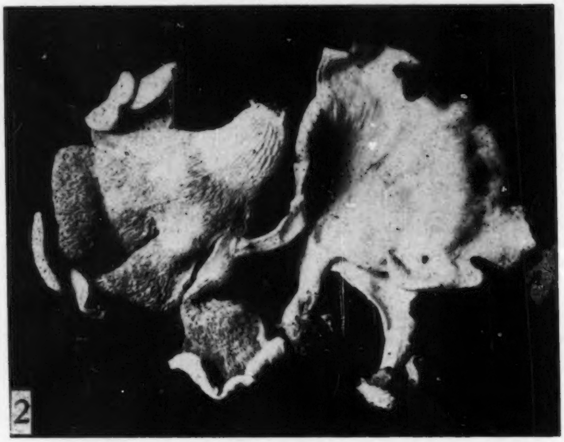

Fig. 2.—*Favolus brasiliensis* Fr. X ¾.

2. Pores usually equally hexagonal; spores 14-20 X 5-8μ........*F. cucullatus*
2. Pores radially elongate; spores smaller 3
3. Pileus reniform, reddish at first; stem usually reduced..............*F. alveolaris*
3. Pileus reniform to flabelliform, never reddish; stem usually distinct ....*F. brasiliensis*

1. *F. alveolaris* (D.C. ex Fr.) Quél.—Overholts lists this species as occurring in Alabama and Georgia. Therefore, it is not surprising to find that it also occurs in Louisiana.

Specimens: 4 VII 56, WF; 27 I 57, A; 10 III 57, EBR; 13 IV 57, L.

2. *F. basiliensis* Fr.—Fig. 2. The species is not uncommon and is found usually in massive clusters on oak stumps.

Specimens: 15 V 56, EBR; 13 X 56, St.L, ALW 294; 14 X 56, I, ALW 260; 19 III 57, P; 19 III 57, EBR; 24 III 57, St.C, ALW 285; 2 V 57, WF; 2 VI 57, EBR.

3. *F. cucullatus* Mont.—An uncommon species. It is easily recognized by its pigmentation which is quite similar to *Mycobonia flava*. Overholts lists the species from Georgia and Florida but not from Louisiana.

Specimens: 5 VIII 56, EBR; 13 VIII 56, EBR, ALW 275.

4. *F. Rhipidium* (Berk). Sacc.—Pure white to slightly yellowish when fresh, drying yellowish. The pores are thick walled and pubescent because of botryoid hyphae borne on the pore mouths. The hyaline, smooth spores are 4-5 X 2-3μ.

Specimens: 18 VIII 56, J, ALW 259; 3 IX 56, St. L, ALW 238; 2 V 57, WF; 5 VII 57, A; 25 X 57, EBR.

FOMES (Fr.) Kickx

Pores usually arranged in distinct layers because of perennial growth of sporophore; usually extremely hard and woody when dry; spores are smooth, hyaline to brown. The species with usually truncate spores appearing echinulate are treated with *Ganoderma*. Of the thirteen species of *Fomes* reported from Louisiana, we have collected only two.

1. Pileus without crust; tubes not distinctly stratified in some specimens, but sporophore hard and woody when dry .... *F. geotropus*
1. Pileus with grayish crust, tubes distinctly stratified .... *F. marmoratus*

1. *F. geotropus* Cooke.—Typically, this species is a Gulf State fungus, although it has been reported from Missouri and Arkansas. Our single collection was made at the base of a deciduous tree near Westwego.

Specimens: 7 II 58, J.

2. *F. marmoratus* (B. & C.) Cooke.—Relatively common.

Specimens: 14 X 56, St.M, ALW 237; 24 XII 56, St.C, ALW 111; 22 IV 57, EBR; 23 IV 56, St. J, ALW 255; 15 IX 57, EBR.

GANODERMA Karst. emend. Pat.

Annual or perennial, stipitate or sessile, leathery to woody. Pileus with a firm crust covering a brown to white contex. Characterized by brown, usually truncate spores which appear echinulate because of the minute spines borne by the endospore.

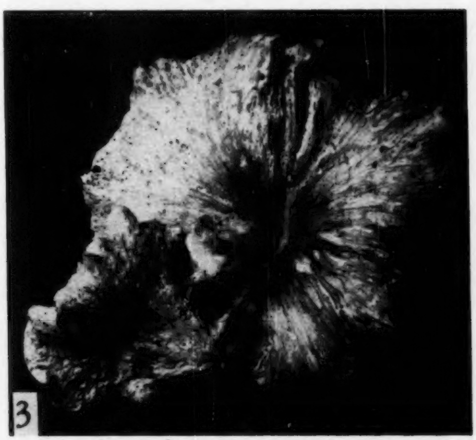

Fig. 3.—*Polyporus virgatus* Berk. & Curt. Upper surface.

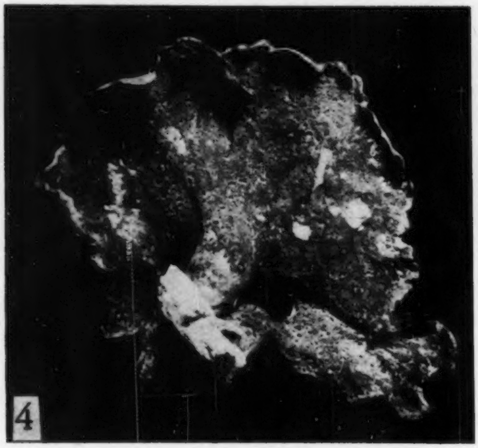

Fig. 4.—*Polyporus virgatus* Berk. & Curt. Pore surface. X ¾.

1. Sporophores usually stipitate 2
1. Sporophores usually sessile 3
   2. Pileus surface bright red to mahogany or black; margin usually acute; in one collection with two layers of tubes ....*G. lucidum*
   2. Pileus surface yellowish brown or olivaceous; margin usually thick and obtuse ....*G. Curtisii*
3. Surface varnished, light red to brownish red or darker ....*G. sessile*
3. Surface not varnished, crust grayish or dark; perennial with new pilei growing out below those of previous year; pores not stratified ....*G. lobatum*

1. *G. Curtisii* (Berk.) Murr.

Specimens: 19 VI 53, G; 25 V 54, EBR; 11 II 56, WF; 23 V 56, W, ALW 53; 29 IX 56, St.T, ALW 258; 13 IV 57, L; 12 V 57, EBR.

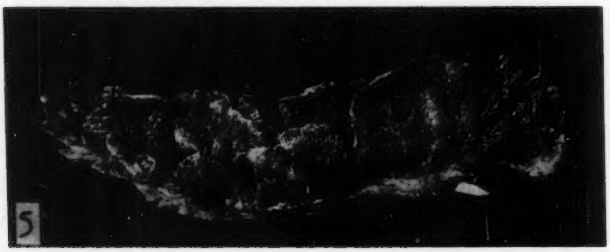

Fig. 5.—*Lezites striata* (Sw. ex Fr.) Fr. Gilled hymenial surface. X ¾.

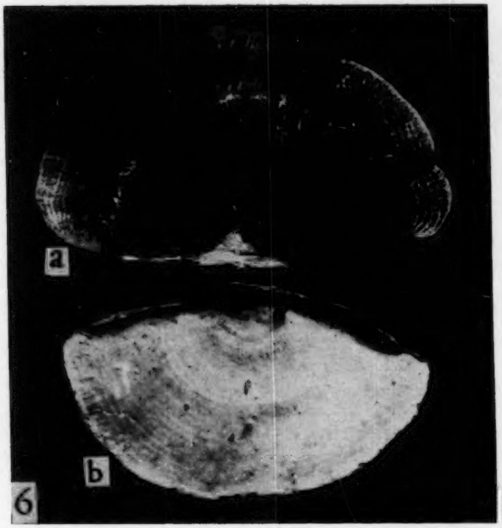

Fig. 6.—*Polyporus hydnoides* Sw. ex. Fr. Two sporophores. a, upper surface; b, pore surface. X ¾.

2. *G. lobatum* (Schw.) Atk. = *Fomes lobatus* (Schw.) Cooke.
Specimens: 22 V 56, W, ALW 54; 23 V 56, T.

3. *G. lucidum* (Leys.) Karst.—A species which may be perennial in the manner of *Fomes*. One collection (1 II 58, St.T) possesses two layers of tubes. A specimen collected on the Tulane campus at the base of an oak is 32 cm wide. This considerable increase in width over typical specimens is caused by new pilei forming from the edges of the older ones. The stipes are in the center of the oldest pileus.

Specimens: 26 VI 52, EBR; 21 IV 53, EBR; 10 VI 55, EBR, L; III 56, EBR, 130 P; 29 IV 56, EBR; 15 VI 56, O; 14 VIII 56, WF, ALW 281; 21 VIII 56, O; 12 X 56, St.T, ALW 224; 9 XI 56, EBR; 18 III 57, EBR; 1 II 58, St.T.

4. *G. sessile* Murr.—Found twice in Orleans Parish on the exposed roots of *Quercus virginiana*. Overholts considers this species as synonymous with *Polyporus lucidus* Leys. ex Fr.

Specimens: 19 I 56, St.T, ALW 257; II 56, St.T, ALW 58; 24 IV 56, O, ALW 251; 31 X 56, O, ALW 235.

HEXAGONA Pollini emend. Fr.

Pores resembling those of *Favolus* except not elongated or arranged in radiating rows. Sporophores are sessile in this genus and stipitate to substipitate in *Favolus*.

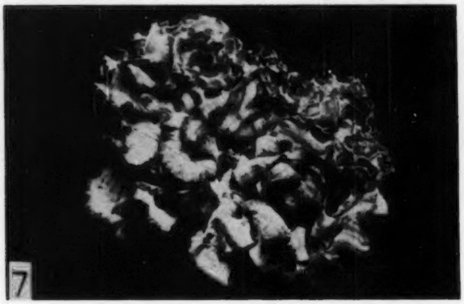

Fig. 7.—*Polyporus frondosus* Dicks. ex Fr. Gaespitose cluster of sporophores. X ¾.

1. *Hexagona variegata* Berk.—Fig. 11. This is the only species of *Hexagona* reported by Overholts from the U.S. (Fla.).

LENZITES Fr.

Sporophores lamellate to somewhat daedaloid. Context usually white, but if hymenium daedaloid, then context brown. Three species of *Lenzites* have been reported from Louisiana. We have failed to find *L. trabea,* but add *L. striata* to the list.

1. Context white to light wood color; pileus strongly pubescent .... *L. betulina*
1. Context umber to rusty brown 2
   2. Sporophore bright rusty brown or umber .... *L. saepiaria*
   2. Sporophore umber or cinnamon; hymenium completely gilled .... *L. striata*

1. *L. betulina* (L. ex. Fr.) Fr.
Specimens: 25 XI 52, EBR; 21 IV 53, EBR; 4 II 56, St. T, ALW 57; 13 III 56, St.T; 4 III 56, WF; 13 VIII 56, EBR, ALW 311, 313; 15 IX 57, EBR; 20 X 57, I.

2. *L. saepiaria* (Wulf. ex Fr.) Fr.
Specimens: 21 IV 53, EBR; 18 VI 53, R, 104 P; 18 III 56, St.T; 4 VII 56, WF; 13 XII 56, EBR; 18 IV 57, W, ALW 252.

3. *L. striata* (Sw. ex Fr.) Fr.—Fig. 5. A common tropical species. Georgia, Florida and Arizona is the distribution cited by Overholts.
Specimens: 19 VI 53, G; 4 VII 56, WF; 8 V 56, EBR, 114 P; 14 VIII 56, WF, ALW 314; 13 X 56, St.L, ALW 240; 15 IX 57, EBR; 20 X 57, I; 1 II 58, St.T.

MERULIUS Haller emend. Fr.

Sporophore usually somewhat gelatinous when fresh, resupinate to pileate. Characterized by shallow folds or pores on the hymenial surface which are fertile over their edges.

1. Sporophore with well-developed, white, dimidiate pileus ..... *M. incarnatus*
1. Sporophore resupinate or with inturned margins, but without well-developed pileus 2
 2. Sporophores fleshy-tremellose, pores large ..... *M. tremellosus*
 2. Sporophores not fleshy-tremellose 3
3. Margins white, hymenial surface pink ..... *M. pallens*
3. Margins golden-yellow, as is the hymenium ..... *M. aureus*

1. *M. aureus* Fr.—A beautiful golden-yellow species often with reddish tints. The margins fold in toward the hymenium giving an open cup-shaped appearance. Not previously reported from Louisiana.
Specimens: 18 II 56, St.T, ALW 17; 23 V 56, W, ALW 19.

2. *M. pallens* Schw.
Specimens: 22 I 56, O.

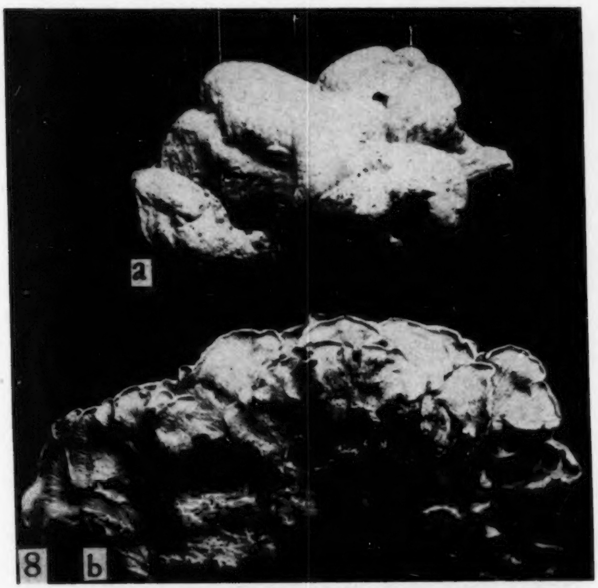

Fig. 8.—*Merulius incarnatus* Schw. a, imbricate pilei seen from above; b, hymenial surface. X ¾.

3. *M. incarnatus* Schw.—Fig. 8. A not uncommon species characterized by the well-developed usually imbricate pileus and the distinctive pink color of the hymenium.

Specimens: 2 II 52, EBR; 18 XII 55, EBR; 29 I 56, EBR; 15 III 57, EBR; 7 II 58, J.

4. *M. tremellosus* Schw.

Specimens: 21 IV 53, EBR; 19 X 54, EBR.

POLYPOROUS Micheli ex Fr.

Sporophore usually annual, stipitate, sessile, or effuso-reflexed; terrestrial or growing on wood; fleshy, tough, leathery, or woody. Context white, bright-colored, to dark brown. Hymenium typically poroid with circular to angular mouths, in old specimens somewhat hydnoid to daedaloid but poroid appearance generally present at margins of pileus. Spores white, brown, even, or roughened.

1. Sporophores stipitate to substipitate 2
1. Sporophores sessile, effuso-reflexed, rarely resupinate 14
    2. Context yellowish-brown to cinnamon; cuticle breaking into radial fibrillose lines exposing the context ....*P. virgatus*
    2. Context white, pale yellow, or wood colored 3

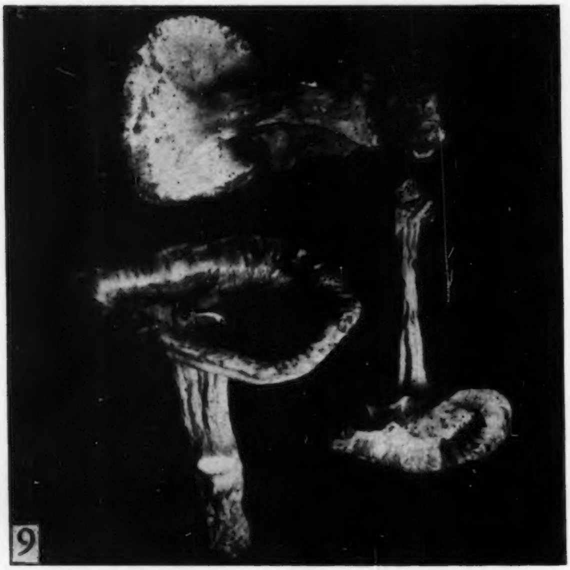

Fig. 9.—*Polyporus dealbatus* Berk. & Curt. Three sporophores. X ¾.

3. Stem black at base .... *P. picipes*
3. Stem not black at base, same color throughout 4
   4. Stem branched giving rise to from few to many pilei 5
   4. Stem unbranched 7
5. Tubes sulphur-yellow; pores 3-4 per mm .... *P. sulphureus*
5. Tubes white or yellowish 6
   6. Pores 1-3 per mm, not turning blackish when bruised or with age .... *P. frondosus*
   6. Pores 4-7 per mm, often becoming blackish when bruised or with age .... *P. giganteus*
7. Pileus usually bearing a cup-shaped sterile structure at the base on the upper surface .... *P. conchifer*
7. Pileus without any such sterile structure on pileus surface 8
   8. Context duplex with soft upper layer and a firm layer next to the tubes .... *P. biennis*
   8. Context not duplex 9
9. Margin of the pileus ciliate 10
9. Margin of the pileus not conspicuously ciliate 11
   10. Pores less than 3 per mm .... *P. arcularis*
   10. Pores 3-6 per mm .... *P. Tricholoma*
11. Pileus multizonate; pores 5-8 per mm 12
11. Pileus azonate or nearly so; sporophore soft and light 13

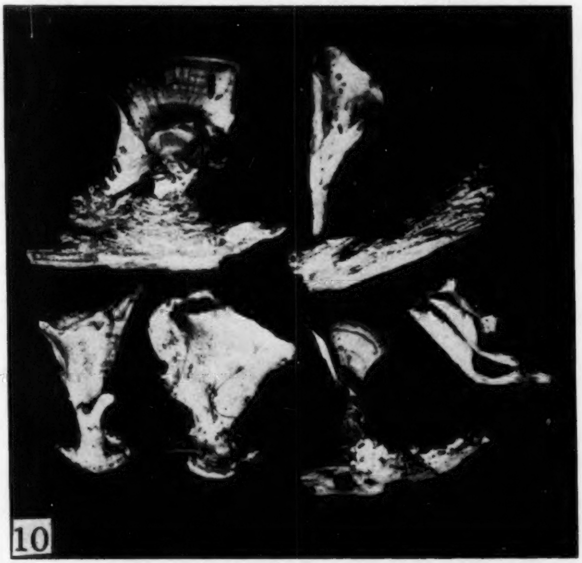

Fig. 10.—*Polyporus mutabilis* Berk. & Curt. Several sporophores, showing upper and pore surface views. X ¾.

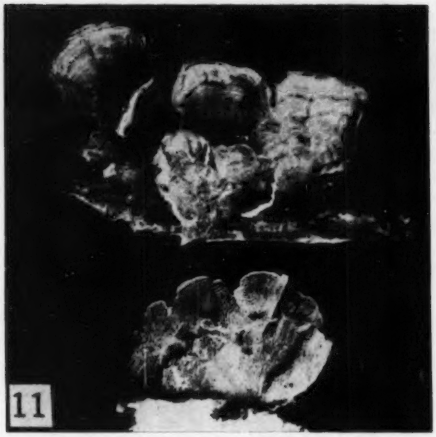

Fig. 11.—*Hexagona variegata* Berk. Above, upper surface; below, pore surface. App. X 1/3.

12. Pore surface flesh-colored; pileus hard and rigid, distinctly stipitate .... *P. dealbatus*
12. Pore surface yellowish, not flesh-colored; stipe not well-developed .... *P. mutabilis*

13. Pileus cinereous, gray, drab .... *P. amygdalinus*
13. Pileus brown, sometimes with lavender tints .... *P. persicinus*

14. Context yellowish-brown or darker 15
14. Context white, bright-colored, or light wood brown 16

15. Pileus covered on its upper surface with stiff, erect, brownish-black hairs .... *P. hydnoides*
15. Pileus villose to glabrous but without hairs such as above .... *P. gilvus*

16. Pileus cinnabar-red 17
16. Pileus variously colored but not cinnabar-red 18

17. Context 4 mm or more thick .... *P. cinnabarinus*
17. Context 3 mm or less thick .... *P. sanguineus*

18. Pileus with cup-shaped sterile structure at the base on its upper side .... *P. conchifer*
18. Pileus lacking such a cup-shaped structure on the upper surface of the pileus 19

19. Tubes of different color or consistency than context 20
19. Tubes of same color and consistency as context 24

20. Pores sulphur-yellow .... *P. sulphureus*
20. Pores flesh-colored, smoke-colored, reddish-purple, purplish-black to black 21

21. Tubes waxy, easily separating from the context, flesh-colored through reddish-purple .... *P. dichrous*
21. Tubes not waxy, smoke-colored through black 22

Fig. 12.—*Daedalia ambigua* Berk. Upper surface of sporophore. Scale shown.

Fig. 13.
Polyporus zonalis Berk.
Upper surface.

22. Tubes purplish, early breaking into teeth; pores 2-4 per mm .... *P. pargamenus*
22. Tubes smoke-colored to black, not breaking into teeth 23
23. Pores 3-4 per mm; tubes smoke-colored .... *P. fumosus*
23. Pores 6-8 per mm; tubes generally black .... *P. adustus*
24. Tubes breaking into teeth early, strongly resembling a hydnoid fungus .... *P. tulipiferae*
24. Tubes may break into teeth after sporophore matures but then not with well-developed teeth 25
25. Pores 1 mm or more wide; pileus azonate .... *P. obtusus*
25. Pores 2-9 per mm; pileus generally zoned but may be azonate 26
26. Pileus azonate, drying soft and light, rigid but not hard .... *P. amygdalinus*
26. Pileus zonate, drying flexible or rigid but not soft and light 27
27. Pileus nearly glabrous 28
27. Pileus villose, pubescent, velvety to the touch 29
28. Pores 4-7 per mm .... *P. Drummondii*
28. Pores 8-9 per mm .... *P. zonalis*
29. Zones on pileus multicolored .... *P. versicolor*
29. Zones, when present, nearly or quite concolorous or with marginal zone darker or lighter 30
30. Pores 3-4 per mm, usually with marginal zone lighter or darker than rest of pileus .... *P. hirsutus*
30. Pores 5-6 per mm, usually with all zones more or less concolorous .... *P. pavonius*

1. *P. adustus* Willd. ex. Fr.—Common on oak and sweet gum. Often fruiting abundantly, covering several meters of dead wood.

Specimens: 24 IV 56, WBR; 4 VII 56, WF; 2 IV 57, St.T; 13 IV 57, L; 25 X 57, EBR; 29 XII 57, EBR; 7 II 58, J.

2. *P. amygdalinus* Berk. & Rav.—From the distribution reported by Overholts this fungus seems to be a typical Gulf Coast species.

Specimens: 17 VII 57, EBR.

3. *P. arcularis* Willd. ex Fr.—A common species on deciduous

wood. Spores hyaline, smooth, apiculate, 8-10 X 3-5μ A species closely related to *P. Tricholoma* (see below).

Specimens: 21 VI 53, P, WBR; 22 V 54, EBR, 11 II 56, WF; 15 V 56, WBR; 14 V 57, WBR; 1, 13 VIII 56, EBR.

4. *P. biennis* (Bull. ex Fr.) Fr.

Specimens: 21 IV 53, EBR; 19 X 54, EBR; 11 II 56, WF.

5. *P. cinnabarinus* Jacq. ex Fr.—A species often confused with *P. sanguineus* (see below) but generally with a thicker context and a more rugulose appearance to the pileus surface.

Specimens: 7 XII 52, EBR; 21 IV 53, EBR; 16 VI 53, EBR; 22 V 54, EBR; 8 X 55, EBR.

6. *P. conchifer* (Schw.) Fr.—This species appears not to have been previously reported from Louisiana.

Specimens: 16 IX 57, EBR; 29 XII 57, EBR.

7. *P. dealbatus* B. & C.—Fig. 9. Previously reported from South and North Carolina. Not common.

Specimens: 22 V 56, W, ALW 106; 14 V 57, EBR.

8. *P. dichrous* Fr.—The easily peeled flesh-colored to reddish-purple tubes characterize this species.

Specimens: 21 IV 53, EBR; 8 X 55, EBR; 19 I 56, T; 29 I 56, St.T; 11 II 56, WF; 24 IV 56, EBR, P 128; 22 V 56, W; 10 VII 56, EBR, P 111; 14 VIII 56, WF, ALW 314; 13 X 56, St.L, ALW 240; 1 II 58, St.T.

9. *P. Drummondii* Klotz.—Overholts reports this species only from Florida and Louisiana. On *Taxodium distichum*.

Specimens: 21 IV 53, EBR; 12 V 57, EBR.

10. *P. frondosus* Dicks. ex Fr.—Fig. 7.

Specimens: 11 II 56, WF; IV 56, EBR, P 126.

11. *P. fumosus* Pers ex. Fr.

Specimens: 22 V 56, W, ALW 239; 13 X 56, St.L, ALW 242; 14 X 56, St.M, ALW 247; 19 IV 57, M, ALW 254; 13 VIII 57, EBR, ALW 280.

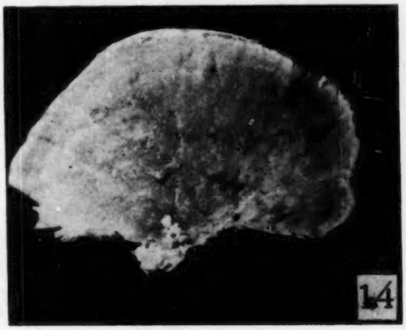

Fig. 14.
Polyporus zonalis Berk.
Pore surface. X ¾.

Fig. 15.—*Polyporus picipes* Fr. Pore surface left, upper surface right. App. X 1/3.

12. *P. giganteus* Pers. ex Fr.—Fig. 1. The specimen shown in the figure was collected by Dr. L. S. Doerpinghaus on dead *Magnolia grandiflora* in a swampy region about five miles south of the Louisiana State University campus. Overholts cites a specimen "that measured thirty-three inches across and weighed thirty-six pounds." These are presumably the dimensions of the fungus when fresh. The dry weight of the collection in Fig. 1 was about 510 grams.

13. *P. gilvus* (Schw.) Fr.—We do not believe it necessary to cite individual collections. The fungus is among the commonest in the region and we feel confident it can be collected in all parishes throughout the year.

14. *P. hirsutus* Wulf. ex Fr.—Common on magnolia, sweet gum and oak.

Specimens: 8 X 55, EBR; 11 II 56, EBR, P 123; 23 V 56, W, ALW 20; 27 V 56, L; 18 IX 56, P; 21 VI 57, EBR; 20 X 57, IV; 1 II 58, St.T.

15. *P. hydnoides* Schw. ex. Fr.—Fig. 6. A characteristic species of the Gulf Coast. Extremely common in southern Louisiana, much more so than is indicated by the specimens listed.

Specimens: 7 VI 52, EBR; 10 II 55, EBR; 16 X 55, EBR, L; 19 I 56, T; 11 II 56, WF; 5 V 56, EBR, P 124; 23 V 56, W, ALW 35.

16. *P. mutabilis* Berk. & Curt.—Fig. 10. Basidia about 8-10 X 5-7μ with four short (less than 2μ) sterigmata. The hyaline smooth spores are 4-5 X 3-4μ with a short apiculus. A relatively common species found on fallen deciduous wood.

Specimens: 26 VI 52, L, P 143; 13 V 56, EBR, P 140; 15 V 56, O; 20 V 56, St.T, ALW 37; 14 VIII 56, WF, ALW 278; 29 IX 56, St.T, ALW 268; 7 X 56, St.T, ALW 267; 14 X 56, St.M, ALW 245; 12 IX 57, EBR; 24 IX 57, EBR; 25 X 57, EBR; 7 II 58, J.

17. *P. paragamenus* Fr.—Very common throughout the region.

Specimens: 15 VII 53, L; 8 X 55, EBR; 4 II 56, St.T, P 112; 4 II 56, St.T, ALW 55; 23 V 56, W, ALW 34 (tan form); 21 VIII 56, St.T (lavender form); 5 X 56, EBR; 9 XI 56, EBR; 29 I 56, EBR, P 127; 4 I 58, EBR.

18. *P. obtusus* Berk.—Spores hyaline, smooth, 7 X 3-4μ Hyphae without clamp-connections.

Specimens: 24 V 56, St.H, ALW 277.

19. *P. pavonius* (Hook.) Fr.—Another typical Gulf Coast fungus. Reported only from Florida and Louisiana.

Specimens: 19 IV 57, M, ALW 253.

20. *P. persicinus* Berk. & Curt.—Figs. 16-17. A relatively rare species collected only two or three times according to Overholts. This is a first report from Louisiana. The brown tomentose sporophore, which is light and spongy when dry, is characteristic. When fresh, the fungus is water-soaked.

Specimens: 12 V 56, St.T, ALW 148 (det. by W. A. Murrill).

21. *P. picipes* Fr.—Fig. 15. Previously unreported from Louisiana. Stipitate, infundibuliform sporophores with pores about 5 per mm are typical.

Specimens: V 56, EBR, P 129, III 57, EBR.

22. *P. sanguineus* L. ex Fr.—Extremely common in the Gulf States and easily recognized because of its cinnabar-red, smooth pileus and thin context. Generally southern in distribution. Its northern counterpart is *P. cinnabarinus* (see above).

Specimens: 15 V 52, EBR; 15 VII 53, P 117; 11 II 56, WF; 5 V 56, St.T; 15 V 56, EBR; 23 V 56, T, ALW 36, 56; III 57, EBR.

Fig. 16.—*Polyporus persicinus* Berk. & Curt. Upper surface.

Fig. 17.—*Polyporus persicinus* Berk. & Curt. Pore surface. App. X 1/3.

23. *P. sulphureus* Bull. ex Fr.
Specimens: 15 XII 57, O, coll. by D. C. Hardy.

24. *P. Tricholoma* Mont. Overholts reports this species only from Texas. It has been collected abundant in southern Louisiana. *P. Tricholoma* and *P. arcularis* may well be synonymous. The only major distinction seems to be the smaller size of *P. Tricholoma.*
Specimens: 21 I 55, EBR; 18 IV 56, Wb, ALW, 256 (dark form); 30 V 56, St.T, ALW 32; 24 III 57, St.C, ALW 283, 284.

25. *P. tulipiferae* (Schw.) Overh. [*Irpex lacteus* Fr.]—Not previously reported from Louisiana.
Specimens: 13 VIII 56, EBR, ALW 250.

26. *P. versicolor* L. ex Fr.—Very common.
Specimens: 29 IV 52, EBR; 15 VII 53, P 117; 11 II 56, WF; 13 VIII 56, EBR; 3 IX 56, EBR, L; 29 IX 56, St.T, ALW 271; III 57, EBR; 1 II 58, St.T; 7 II 58, J.

27. *P. virgatus* Berk. & Curt.—Figs. 3-4. This species was first collected in Cuba and described by Berkeley and Curtis in 1868. Lloyd (1912), referring to it under the name *Lentus virgatus,* indicates that it is only "known from one abundant collection from Cuba." It was collected in Florida in 1911 and Overholts (1952) states that "no other than the Florida collection is known from the United States." Four collections were made in one locality in East Baton Rouge Parish; the collection date of the specimen figured was 13 IX 56. Microscopically, the Louisiana material conforms closely with the description given by Overholts (p. 267). No spores were found.
Specimens: 30 V 56, EBR, P 131; 13 IX 56, EBR; 28 IV 57, EBR; 31 VIII 57, EBR.

28. *P. zonalis* Berk. Figs. 13-14. Reported only from Florida, Louisiana and Mississippi.

TRAMETES Fr.

Sporophores leathery to corky, sessile to resupinate. Context white to brown. Pores seated at various depths in the context, thus not forming a continuous straight line at their bases. Only two of the five species reported from Louisiana by Overholts have been collected.

1. Pileus 0.5 cm or less thick, thin and coriaceous, sometimes resupinate, often effuso-reflexed with a narrow, free margin .... *T. rigida*
1. Pileus 2-5 mm thick, never resupinate and pileus well developed .... *T. malicola*

1. *T. malicola* Berk. & Curt.—Spores 9 X 3μ.
Specimens: 24 III 57, St.C, ALW 290.

2. *T. rigida* Berk & Mont. A species generally limited to the tropics and subtropics. It is very common in the Gulf States, often assuming a resupinate growth form. Even when well-developed the sporophore produces only a very narrow pileus.

Specimens: 15 VI 56, O, ALW 249, 265; 2 II 57, EBR; 4 III 57, J, ALW 289; 24 III 57, St.C, ALW 283a; 1 IV 57, J, ALW 291.

LISTS OF POLYPORES REPORTED FROM LOUISIANA[2]

Featherman (1871, 1872)

Polyporus beisulcis Fr.
Polyporus seraposus Fr.

Langlois (1887)

Hexagona sericeo-hirsuta Klotz. = *Polyporus pinsitus* Fr. (fide Overh.)
Lenzites corrugata Klotz.
Merulius corium Fr.
M. subchlorinus Ell. & Lang.
Polyporus abietinus Fr. = *F. abietinus* Dicks. ex Fr. (fide Overh.)
P. abortivus Pk. = P. biennis (Bull. ex Fr.) Fr. (fide Overh.)
P. callosus Fr.
P. carneus Nees
P. chartaceus B. & C. = *P. biformis* Fr. (fide Murr.)
P. cinereus Schw.
P. coesius Schrad.?
P. ectypus B. & C.
P. epileucus Fr. ?
P. eroccatus Lév.
P. Feathermanii (without citation) = *P. hydnoides* Sw. ex Fr. (fide Overh.)
P. floridanus Berk. = *P. sector* Ehrenb. ex. Fr. (fide Overh.)
P. hemileucus B. & C. = *P. supinus* Sw. ex Fr. (fide Overh.)
P. lacteus Fr. = *P. albellus* Pk. (fide Overh.)
P. leucomelas Pers.
P. licnoides Mont.
P. Lindbladii Berk.
P. molluscus Fr.
P. nitidus Fr.
P. obliqus Fr.
P. plebeius Berk.
P. pidilis Berk.
P. purpureus Fr.
P. radiatus Fr.
P. rufescens Fr. = *P. biennis* (Bull. ex. Fr.) Fr. (fide Overh.)
P. sinuosus Fr.
P. spissus Schw. ?
P. spumeus Fr.
P. Stephensii Berk.
P. sublutescens E. & E.
P. tabacinus Mont.
P. tenellus Berk. & Curt.
P. umbonatus Fr.
P. vaporarius Fr.
P. velutinus Fr.
P. violaceus Fr. ?
P. vitellinus (without citation)
P. vulgaris Fr.
Trametes lactea Fr. ? = Daedalia ambigua Berk. (fide Overh.)

Overholts (1953)

Daedalia Berkeleyi Sacc.
D. confragosa L. ex Fr.
D. unicolor Bull. ex Fr.
Fomes annosus (Fr.) Karst.
F. Calkinsii (Murr.) Sacc. & D. Sacc. = *F. robustus* Karst. (fide Lowe)
F. densus Lloyd = *F. conchatus* (Pers. ex Fr.) Gill. (fide Lowe)
F. fraxineus (Bull. ex Fr.) Cooke
F. Meliae (Underw.) Murr.
F. robustus Karst.
F. Langloisii (Murr.) Sacc. & D. Sacc. = *F. robustus* Karst. (fide Lowe)
F. rimosus (Berk.) Cooke = *F. robiniae* (Murr.) Sacc. & D. Sacc. (fide Lowe)
Lenzites trabea Pers. ex Fr.
Polyporus abietinus Dicks. ex Fr.

[2] Individuals of the species reported in the lists were not encountered by us. The genus *Merulius* is included; *Poria* is omitted.

P. anceps Pk.
P. Berkelei Fr.
P. biformis Fr.
P. cinnamomeus Jacq. ex Fr.
P. crocatus Fr.
P. cuticularis Bull. ex Fr.
P. dryadeus Pers. ex Fr.
P. Dryophilus Berk.
P. durescens Overh.
P. ectypus Berk. & Curt.
P. fasicola Berk. & Curt.
P. fimbriatus Fr.
P. fissilis Berk. & Curt.
P. fociola Berk. & Curt.
P. galactinus Berk.
P. hispidus Bull. ex Fr.
P. iodinus Mont.
P. licnoides Mont.
P. Ludovicianus (Pat.) Sacc. & Trott.
P. maximus (Mont.) Overh.
P. mollis Pers. ex Fr.
P. nidulans Fr.
P. palustris Berk. & Curt.
P. pinsitus Fr.
P. porrectus (Murr.) Sacc. & Trott.
P. rigidus Lév.
P. Schweinitzii Fr.
P. sector Ehrenb. ex Fr.
P. semipileatus Pk.
P. Spraguei Berk. & Curt.
P. subectypus (Murr.) Bres.
P. submurinus (Murr.) Lloyd
P. supinus Sw. ex Fr.
P. tenuis (Sacc.) Overh.
P. versatilis (Berk.) Rom.
P. vinosus Berk.
Trametes cubensis (Mont.) Sacc.
T. hispida Bagl.
T. sepium Berk.
T. serialis Fr.

Burt (1917)
Merulius americanus Burt
M. brassicaefolius Schw.

SUMMARY

Based upon the lists published by Featherman, Langlois, and Overholts, approximately 113 species of polyporaceous fungi (excluding *Poria* but including *Merulius*) have been reported from Louisiana. Several names used by earlier authors are pre-Fresian and may be synonyms which we are, at present, unable to trace. Ten species, hitherto unreported from the state, are included in this report, bringing the total to 123 species, of which 49 are listed here. Such a large number undoubtedly places Louisiana among the richest areas in species of polypores.

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REFERENCES

BURT, E. A. 1917—*Merulius* in North America. Ann. Mo. Bot. Gard. **4**:305-362.

FEATHERMAN, A. 1871—The Botany of Louisiana. 2d Annual Report of the Botanical Survey of Southern and Central Louisiana. Pp. 123-131. New Orleans.

———1872—3rd. Annual Report of the Botannical Survey of Southwestern and Northwestern Louisiana. Pp. 101-161. New Orleans.

LANGLOIS, A. B. 1887—Catalogue Provisoire des Plantes Phanérogames et Crytogames de la Basse-Louisiane. Pinsard-Bongrand. Saint-Eitienne.

LLOYD, C. G. 1912—Synopsis of the Known Polyporoids. Mycological Writings **3**:95-208.

LOWE, J. L. 1957—Polyporaceae of North America. The Genus *Fomes.* State Univ. Coll. Forestry, Syracuse.

MURRILL, W. A. 1907, 1908—(Agaricales) Polyporaceae. North American Flora. **9**. Pt. 1, 1907. Pt. 2, 1908.

OVERHOLTS, L. O. 1953—The Polyporaceae of the United States, Alaska, and Canada. Univ. Mich. studies. Sci. Series, Vol. 19. Pp. 466.

Geographic Variation in the Wood Frog
Rana sylvatica

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The nomenclatural history of *Rana sylvatica* is beset with considerable instability. This instability directly reflects the general absence of adequate criteria for recognition of species and subspecies. More specifically it reflects the absence of a comprehensive study of this species.

Rana sylvatica was first described by Le Conte in 1825. Almost simultaneously, Harlan (1826) described this species as *Rana pennsylvanica;* however, the latter has been designated a *nomen nudum.*

Baird (1854) described *R. cantabrigensis.* He noted that it was closely related to *R. sylvatica* and differentiated it on the basis of the length of tibia, that was half the body length, and on the presence of a middorsal light stripe that extended from snout to vent.

Impressed by the resemblance in size and general coloration of the American *R. sylvatica* and *R. cantabrigensis* to each other and to the Eurasian *R. temporaria,* Cope (1875) concluded that they were subspecies of *R. temporaria.* Later, Cope (1886) described an Alaskan race and then chose to designate *sylvatica* and *cantabrigensis* as species, the new Alaskan race being *R. c. latiremis.* This subspecies was distinguished from the type race by having two, instead of three, phalanges free of web on the hind foot and by the absence of the dorsal stripe. Nomenclaturally it is interesting that Cope (1889) later referred to a "variety," *R. c. evittata,* which was somewhat intermediate between the two races earlier established. It was characterized by the presence of three free phalanges and by the absence of the dorsal stripe. "It is also found at several localities mingled with the typical form, though this is not always the case. Judging from the collection in the National Museum, it is as abundant as the typical variety." As is obvious, it is difficult to ascertain what differences, if any, existed in Cope's mind as to the distinction between a variety and a subspecies. Fortunately, none of the subsequent workers referred to Cope's *R. c. evittata.*

Howe (1899) greatly clarified the status of *R. cantabrigensis.* He examined a large series of New England wood frogs and concluded that the type locality could not possibly have been Cambridge, Massachusetts, as stated by Baird. Instead he thought that Baird's type was probably from the northwestern part of North America and that the selection of Cambridge as the type locality arose solely because the specimen was in the collection of Professor Agassiz. Further support for Howe's conclusion was provided by his finding in a collection from Saskatchewan, Canada, an old, shrunken, unlabelled specimen which conformed closely to the description of the type.

In specimens from various areas of the Hudson Bay Region, Preble (1902) noted a difference in the relative length of the hind legs. This important observation continued to be ignored for the next several decades.

Boulenger (1920) distinguished *R. sylvatica* from *R. cantabrigensis* by whether the tibio-tarsal articulation extended beyond the eye when the leg was flexed against the body. He noted that these two species were closely related to each other and that their similarity to *R. temporaria* was "a case of independent, parallel evolution in the two parts of the world from a common ancestor."

Stejneger and Barbour (1923) placed *latiremis* in synonymy with *R. cantabrigensis;* however, Schmidt and Necker (1935) recognized *latiremis* as a valid subspecies. In so doing, they were motivated by their difficulty in differentiating *R. cantabrigensis* and *R. sylvatica.* They observed that frogs from the Chicago region had a tibia which was more than half (varying from .54 to .57) of the body length and hence well within the established range for typical *R. sylvatica.* On the other hand, their specimens resembled *R. cantabrigensis* in color pattern (as outlined by Wright and Wright, 1933). Preferring to use color pattern rather than relative length of leg, Schmidt and Necker accordingly allocated these frogs to *R. cantabrigensis.* At the same time they stated that "Wood frogs from Alaska, Canada, and Labrador are much shorter legged than these middle western specimens, and we feel justified in reviving *Rana cantabrigensis latiremis* Cope for them." Later, after a somewhat detailed study of leg length gradients, Schmidt (1938) relegated *cantabrigensis* and *latiremis* to subspecies of *R. sylvatica.*

Trapido and Clausen (1938) noted that the color pattern as employed by Wright and Wright (1933) was not constant enough to separate *cantabrigensis* and *sylvatica.* Independently of Schmidt they concluded that on the basis of relative leg length there was no sharp break between these two forms; accordingly they are best regarded as subspecies. Emphasizing the correlation of relative leg length to north-south distribution and furthermore the variability of color pattern in *cantabrigensis,* Trapido and Clausen did not recognize *latiremis.*

Patch (1939), after examining 90 frogs from various parts of Canada, concurred with Trapido and Clausen. On the basis of whether the leg, minus the foot, was longer or shorter than the body, *sylvatica* was now thought to occur in Nova Scotia, New Brunswick, the Gaspé Peninsula, southern Quebec and southern Ontario westward around Lake Superior and southward through the Appalachians; *cantabrigensis* occurred to the north of this area.

From a study of southwestern Quebec specimens, Grant (1941) concluded that it was inadvisable to assign subspecific rank to the wood frog. Wright and Wright (1942) preferred to agree with Schmidt in recognizing three races, but continued to adhere to the .50 proportion of tibia and body length as the basis for distinguishing *sylvatica* and *cantabrigensis.* This status was further entrenched by

Stejneger and Barbour (1943) who also recognized three races and clarified their ranges as follows: *sylvatica* — similar to that described by Patch; *cantabrigensis* — Alaska, through the lowlands eastward to Michigan, north to the mouth of the Yukon; *latiremis* — Alaska to Labrador. In spite of these apparent clarifications, much uncertainty existed regarding these subspecies and their respective ranges.

Breckenridge (1944) noted that, according to the proportions suggested by Wright and Wright (1942), Minnesota specimens are best classified as *sylvatica,* but on the basis of whether the leg, minus the foot, is longer or shorter than the body, they are best classified as *cantabrigensis.*

After a careful study of Ohio specimens, Walker (1946) separated them into *R. s. cantabrigensis,* i.e., those in the northwestern corner of the state with a tibia length of .53 or less of the body length and with more or less dusky pigment between the dorso-lateral folds; and *R. s. sylvatica,* i.e., those occurring in the remainder of the state, having a tibia length of .54 or more of the body length and with little or no dusky mottling between the dorso-lateral folds.

In 1947, Maslin reported wood frogs in the Rocky Mountains of Colorado and assigned them to *R. s. cantabrigensis.* Furthermore he attempted unsuccessfully to revive *latiremis.* He thought that "*R. s. latiremis* may be described as a relatively stocky frog with a tibia-body proportion of .45 or less, a leg to heel measurement equal to or shorter than the body, two phalanges free of web, and lacking the dorsal longitudinal light stripes of body and legs. *R. s. cantabrigensis* is a frog with a tibia-body proportion ranging from .45 to .55, a leg equal to or shorter than the body length, 2 or 3 phalanges free of web, and possessing at least a dorso-median light body stripe. *R. s. sylvatica* is a frog with a tibia-body proportion of more than .55, a leg length greater than the body length, 3 phalanges free of web, and lacking both a dorso-median light stripe and stripes on the legs."

Wright and Wright (1949) followed Walker's admirable conclusion regarding the diagnostic characteristics which separated *sylvatica* and *cantabrigensis* but insisted on maintaining the boundary between the two forms farther to the north. They distinguished *cantabrigensis* on the basis of its having a mid-band of darker color within the light dorso-lateral folds, middorsal light stripe present or absent, breast spotted, hind limb short, tibia .53, or less, of the body length. *R. sylvatica* was characterized by the absence of a mid-band of darker color between the dorso-lateral folds, no mid-dorsal stripe, breast usually without spots, leg long, and tibia more than .53 of the body length.

In a study of Wisconsin frogs, Suzuki (1951) applied these characteristics and stated that frogs "with *R. s. sylvatica* characteristics are widely distributed throughout the state; whereas, those characteristic of *R. s. cantabrigensis* are more prevalent in the northern half of the state." He concluded that Wisconsin is probably an area of intergradation of the two subspecies.

Schmidt (1953) recognized the ranges of the two subspecies as

follows: *sylvatica* — eastern North America, north to Labrador, south to Georgia in the Appalachians, west to southern Illinois and Arkansas; *cantabrigensis* — mouth of the Yukon and the Mackenzie delta to western Ontario, south into northern Minnesota, Wisconsin, and the Northern Peninsula of Michigan. Finally Witschi (1953) added to the existing confusion by describing, on the basis of larger body size, a new subspecies, *R. s. cherokiana,* from the southern Appalachian Mountains.

It should be noted that most investigators have been primarily interested in a local situation and that none has considered the variation within the entire range of the species. The primary objective of this study is the investigation of variation throughout the range of the species.

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METHODS

We realize that if collections of specimens are to serve as a basis for the determination of the amount and kind of variability within a species, or within any of its parts, the collections must have been made at random (Dice, 1952). For most species, especially those with large geographic ranges, it is impossible to meet this requirement. Accordingly, we made a vigorous attempt to obtain as many specimens as possible. In general, a reasonably good coverage of the range of *R. sylvatica* was represented by the 2,801 specimens assembled. Their distribution, is presented in Table I. As is evident, the samples are not random; furthermore, incongruities occur; e.g., there are 801 specimens from Ontario but only 14 from Quebec.

TABLE I.—Number and distribution of specimens examined

United States					1581
	Arkansas	8	New Jersey	9	
	Colorado	16	New York	54	
	Georgia	30	North Carolina	34	
	Illinois	60	North Dakota	42	
	Indiana	64	Ohio	183	
	Kansas	1	Pennsylvania	100	
	Kentucky	16	South Carolina	3	
	Maine	89	Tennessee	1	
	Maryland	16	Vermont	2	
	Massachusetts	69	Virginia	6	
	Michigan	204	Washington (?)	7	
	Minnesota	199	West Virginia	60	
	Missouri	5	Wisconsin	77	
	Montana	2	Wyoming	12	
	New Hampshire	25	Alaska	187	
Canada					1220
	Alberta	137	Nova Scotia	12	
	British Columbia	51	Ontario	801	
	Labrador	18	Prince Edward Is.	2	
	Manitoba	98	Quebec	14	
	New Brunswick	4	Saskatchewan	39	
	Northwest Terr.	32	Yukon Terr.	12	
Total					2801

All adult specimens were measured for body length, i.e., the distance from the tip of the snout to the distal end of the urostyle, and for tibial length, the maximum length of the tibiofibula when the shank is completely flexed upon the thigh. Measurements were made with vernier calipers and recorded to the nearest tenth of a millimeter. To assure consistency the same person (RLH) made all the measurements.

The sex of all mature specimens was generally ascertained by observation of the secondary sexual characteristics; however, since these vary seasonally in their development it was necessary to dissect many specimens, especially those from northern localities.

Furthermore, the specimens were closely observed as to the nature and markings of the dorso-lateral folds, the markings of the dorsum, venter, and sides of the body, the presence or absence of the pectoral spot, the number and nature of the tibial markings, and the distribution and number of warts and dorsal rugosities.

In conjunction with the quantitative, analytical evaluation outlined above, the specimens were individually classified according to their combined phenotypic characteristics, i.e., according to the total impression derived from their general appearance (coloration, markings, size).

Most of the above-mentioned data are presented on maps. In so

doing, we made no attempt to group specimens collected in the same geopolitical area. Such a procedure was considered too artificial and too inaccurate. Furthermore, variation was analyzed independently of the established boundaries of the recognized subspecies. Because of the wide distribution of *R. sylvatica* and because of the relatively few specimens involved, the maps here included do not show local conditions with the exactitude one would like to have. For example, the equal value contour lines on these maps have been rounded out because of the irregular distribution and varied nature of the collections examined; accordingly local deviations are not indicated. On the other hand, these maps are a good index of the general distribution of the characters considered.

RESULTS AND DISCUSSION

DISTRIBUTION

The geographic range of *R. sylvatica* is large, approximately 4,044,000 square miles; among North American frogs it is exceeded only by *R. pipiens*. From Alaska, the wood frog ranges eastward into Labrador and southward into British Columbia, Colorado, North Dakota, Arkansas, and Georgia. (Fig. 1). Perhaps the most outstanding feature of *sylvatica,* as shown by its distribution, is its tolerance of low temperature and short season of activity. For example, in the lower Mackenzie Valley the frost-free season lasts only about forty days (Kendrew, 1953). Actually the wood frog is the sole North American amphibian known to occur within the Arctic Circle. Not only is it the one amphibian that inhabits the Eskimoan biotic province (as outlined by Dice, 1943), but also it occurs in the Sitkan biotic province, where formerly it was thought not to exist (Oliver, 1955). We have examined specimens taken in the latter province from the following locations in Alaska: Sergief Island (north of the Stikine River), Palmer (in the Matanuska Valley), Kenai, and Yakatat. These localities are widely scattered and indicate that wood frogs range throughout the entire province.

The northern boundary of *sylvatica's* range appears to be limited by temperature and by the distribution of available habitat. Presumably, temperature limits northward migration by not permitting sufficient time for tadpoles to metamorphose and abandon ponds which freeze solid with the onset of winter. Generally the northern limit of the range is that of wooded country; however, there is evidence that they do occur north of the tree line and possibly in the tundra region. This is substantiated by a collection of ten specimens from Cape Henrietta Maria, Ontario — about fifty miles poleward from the northern tree limit. This situation was greatly clarified by Sherman Bleakney (pers. com.) who stated that small wooded areas are located in isolated depressions north of the generally established tree line. There are numerous records of specimens taken near the tree line, among these are: (Localities marked with an asterisk are within the

Arctic Circle.) Beetles,* Kobuk*, Fort Yukon,* Alaska; Great Slave Lake, Husky River below Peel River,* MacKenzie River Delta,* Northwest Territories; Churchill, Manitoba; Fort Chimo, Quebec (Hildebrand, 1949); and Okak, Labrador (Weiz and Packard, 1866). The absence of frogs from the eastern coast of Labrador is undoubtedly due to the effects of the cold Labrador current. It is of interest that amphibians are not native to Newfoundland, Greenland and Iceland (Wynne-Edwards, 1952).

Northern frogs, particularly those from the Alaska-Yukon area, were impressive because they were gorged with food, mainly beetles and other insects. Their stomachs usually were so distended, that these had to be emptied before the gonads could be located and sex ascertained. Apparently northern frogs must feed extensively during their short activity season in order to provide the energy supplies and building materials needed for growth and reproduction and for enduring the long winter.

To the east and west, the distribution of *R. sylvatica* is limited by the Atlantic and Pacific Oceans. No amphibians, except possibly *Bufo marinus* and *Rana cancrivora,* occur in the marine habitat. Evidently the osmoregulatory mechanisms of most amphibians are not adequate to cope with the hypertonic sea water.

Temperature and availability of habitat operate to limit the southern distribution of *sylvatica.* The work of Moore (1949) suggests that temperature operates in the following manner. The embryonic stages of frogs are the least resistant to temperature extremes. Thus, in regions where high temperatures occur, the cold-adapted *sylvatica* provides a "northern" environment for its embryos by spawning during that part of the year when low temperatures prevail. Accordingly as one goes southward through the range, the spawning season occurs

TABLE II.—Spawning records for *Rana sylvatica*

Locality	N. Lat.	Spawning Date
Great Bear Lake-lower Mackenzie River Northwest Terr. (Preble, 1908)	65	May thru July, mainly June
Fort Chimo, Quebec (Hildebrand, 1949)	58	June 21
Tupper Creek, British Columbia (Cowan, 1939)	56	May 9
Nova Scotia (Bleakney, 1952)	45	Late April
Southern Ontario (Logier, 1952)	44	Early April
Southern Michigan (Martof, unpublished)	42.5	Late March-early April
New York (Wright and Wright, 1949)	42.5	Late March-early April
West Virginia (Wilson, 1945)	39	Feb. 20
Georgia-North Carolina	35	January-early February

earlier and earlier in the year (see Table II). It is possible that the southern limit of this "northern" environment is reached in the southern tip of the Appalachian and Ozark Mountains. Breeding occurs there during January and early February, the coldest part of the year; whereas farther north breeding occurs after the coldest part of the year. In the south, only the cool mountain ponds provide the low temperatures required for proper development of the embryos and larvae.

In the southeast, the Appalachian Mountains mark the eastern edge of the range. Wood frogs are known from the Piedmont Region of Virginia, but not of North Carolina, South Carolina, and Georgia. The southernmost records are from Georgia.

West of the Appalachians, this species is known from several scattered localities in Kentucky; apparently it occurs throughout most of that state. In addition to occurring in the Smoky Mountains of Tennessee, wood frogs have been reported farther to the west in Campbell, Overton, Putnam, Macon, Robertson, Davidson, and Dickson counties (Gentry, 1955). They have long been known to inhabit the Ozark Mountains of northwestern Arkansas and adjacent southern Missouri. In spite of the general absence of records from eastern Missouri, the Ozark population closely resembles that in the southern Appalachians. Thus if this population is disjunct, it became so rather recently.

From Kansas there is a single specimen taken 15 miles south of Plymouth, Lyons County (Breukelman and Smith, 1946). This specimen shows affinities to eastern populations and represents a local relic population, very likely a by-product of glaciation.

Northward, wood frogs occur throughout Illinois, Wisconsin, and all but the southwestern corner of Minnesota. To the west of Minnesota the records are widely scattered in the United States; however, in Canada they are numerous and many are close to the international boundary. There are records from the eastern half of North Dakota in Stutsman and Rolette Counties, whereas the only records from Montana are those of two specimens taken in 1909 at Billings, Yellowstone County and one from Havre, Hill County.

An old, yet interesting record exists for the state of Washington (USNM No. 5169). Cope (1889) referred to this record, but later workers have ignored it. The original data indicate that the seven specimens were taken at Puget Sound in 1841 by the United States Exploring Expedition. Since that part of the country was then unsettled and also unmapped, no additional information was available. In spite of the general nature of these locality data, it is of great interest that no recent specimens have been reported in the Washington area! Accordingly, these specimens are probably mislabelled as to locality.

To the south, specimens have been taken in southern Wyoming, Albany County, and in the northern part of Colorado, Jackson County. Because of their resemblance to specimens taken in North Dakota and in southern Saskatchewan and Alberta, it seems probable that

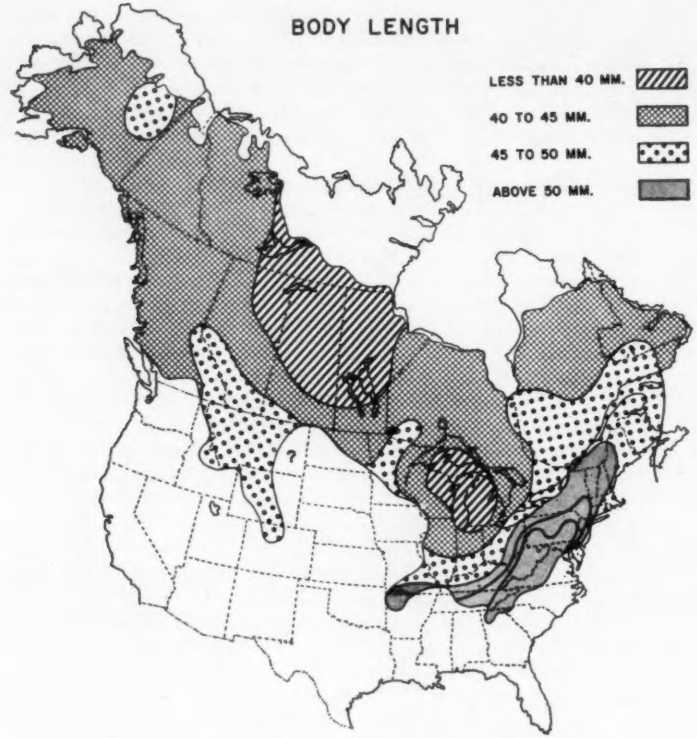

Fig. 1.—Variation in average body length. Isophenes are drawn for a 5 mm interval.

wood frogs occur in some of the intervening ranges of the Rockies and Bitterroot Mountains — even though none has been reported in recent years.

In summary, *sylvatica* ranges northward to about 69 degrees latitude — the farthest north of any cold-blooded tetrapod in the Western Hemisphere. In the Eastern Hemisphere this record is exceeded only by the closely related *R. temporaria,* which reaches the northern limit of land in Scandinavia at about 71 degrees North. The studies by Moore (1949) have strongly indicated that, of the American ranids, *sylvatica* possesses the genotype best suited for survival at low temperature. It breeds very early in its activity season and produces globular, submerged egg masses—well suited for survival in waters where surface freezing often occurs. Its eggs are relatively large; they are provided

with an abundance of yolk. Furthermore, the early larval stages are very tolerant of low temperature and develop at a rapid rate. In addition to permitting *sylvatica* to range far to the north into regions unoccupied by other amphibians, these specializations have imposed a limit on its southern distribution, restricting it to the cooler, wooded areas.

BODY LENGTH

Geographic variation in body size is shown in Figure 1. In order to account for sexual dimorphism in body size (well developed in this species), we first considered only the large samples containing adequate representation of sexually mature males and females. The mean body size and the standard deviation of these representative samples formed the framework of the study; after this the smaller samples were considered. Those samples which contained specimens predominantly of one sex were compared with adjacent samples but the sexes were considered separately. These data were further supplemented by measurements of the largest male and the largest female contained in the various series. By the above procedure, some sampling errors were obviated. These data were plotted on a large map and isophenes (equal value contour lines) were drawn. This method permitted the data to be integrated and condensed, thus expediting their presentation in this report.

The largest wood frogs are found in the southern Appalachian Mountains. Specimens from the Georgia-North Carolina region averaged as follows: 58 females, 66.8 mm; 39 males, 54.8 mm. The largest individuals encountered in this study were from Cherokee County, North Carolina, female 78.8 mm, male 62.5 mm. The largest recorded wood frog is a female from Linnville, Avery County, North Carolina; she measured 82.5 mm (Wright and Wright, 1949). To the northeast of the southern Appalachians, i.e., in New England, Quebec, and Labrador, body size decreased gradually. This is in sharp contrast to the steep gradient which occurs to the west of the Appalachian Mountains, i.e., in Ohio, Kentucky, and Tennessee.

The smallest wood frogs occur in northern Manitoba, northern Saskatchewan, and the adjacent part of the Northwest Territories. Specimens from this region average about 37.3 mm in body size. The largest male taken at Ilford, Manitoba measured only 40.3 mm; the largest female, from Moraine Bay, Great Slave Lake, Northwest Territories, measured 49.3 mm.

Another region of small frogs occurs in the Upper and Lower peninsulas of Michigan and in the northeastern part of Wisconsin. Smallness of body size is typified by the large collections from the Keweenaw Peninsula, Michigan (average size 38.3 mm, largest male, 43.1 mm, largest female, 48.9 mm) and from Washtenaw County, Michigan (average 38.6 mm, largest male, 41.8 mm, largest female 48.9 mm).

Throughout the Rocky Mountains an extremely weak gradient exists. The frogs from the western part of the United States are only slightly larger than those from Alaska, while frogs from the Yukon-British Columbia area are somewhat smaller than those from localities farther to the north or to the south. A moderately weak gradient occurs over the central and eastern parts of Canada.

A corollary of Bergmann's Rule states that poikilothermous terrestrial animals tend to have individuals in warmer regions larger than those in colder regions (Allee *et al.,* 1949). At most, this notion is substantiated by our study only in a very vague way. In the eastern half of the range, the rule seems to apply somewhat directly; i.e., with an increase in latitude there is a decrease in the mean annual temperature and also a decrease in body size. On the other hand, in the western half of the range there is no correlation of body size throughout this entire area. As might be anticipated, latitudinal changes in body size are partly obscured by altitudinal differences in that part of the range; however, a weak gradient in body size also occurs over the Great Plains, the Central Lowland, and the Laurentian Upland Provinces (as outlined by Lobeck, 1948). Obviously the factors controlling body size are somewhat complex.

Geographic variation in body size is often attributed to the resultant surface-mass relationship of an animal. From this point of view, small body size is advantageous in colder regions because it permits a rapid exchange of heat to take place between an animal and its environment. Accordingly a frog would be very responsive to environmental changes — quickly becoming inactive with the onset of cold weather and promptly becoming active with the resumption of warm weather. In a warm climate the survival value of a rapid response to temperature is somewhat lessened. Here, large size may be of advantage because it brings about a proportionately slower exchange of heat between an animal and its environment. On the basis of this interpretation, one might anticipate that the distribution (general spacing and orientation) of isophenes for body size would be closely correlated with that of the mean isotherms for July, the middle of the season of activity. (Wynne-Edwards, 1952, noted that summer rather than winter temperatures determine the northern limits of amphibians.) However, it is impossible to conclude that body size is mainly a function of the average temperature for any month or of the mean annual temperature.

In addition to being important in a consideration of the influence of temperature, the surface-mass ratio is also important in the consideration of another environmental factor, humidity. Small frogs have a greater tolerance of water loss than do large ones; however, this advantage is more than offset by their faster loss of water by evaporation due to relatively greater body surface (Thorson, 1955). Undoubtedly, humidity plays a paramount role in habitat selection, in part, confining wood frogs to heavily wooded areas where shading permits the retention of much moisture in the leaf litter. Further-

more, humidity, together with temperature, very probably exerts a selective pressure on the body size of amphibians. The distribution of average body size of wood frogs does not appear to correlate closely with climatological data, especially that for rainfall and relative humidity. However, if microclimatological data were available, some insight into the influence of humidity on body size probably would be evident.

In a study of *R. clamitans,* Martof (1956) showed that growth was closely correlated with the mean monthly temperature and the number of hours that the temperature was favorable for feeding, i.e., above 60 degrees F. Thus, the correlation of body size with the duration and quality of the season of the frog's activity rather than with the mean monthly or annual temperatures alone, is more meaningful. It is pertinent that the coldest winters of North America are in the region between Hudson Bay and Alaska and further that Manitoba, especially the northeastern part, has the coldest winters for its latitude (Kendrew, 1953). These long, severe winters imply a relatively short summer and accordingly, a short season of activity for wood frogs. Appropriately this is the region in which the smallest wood frogs occur. Likewise, a similar relationship exists between the large frogs of the southern Appalachian Mountains and the prevailing climate. A long season of activity, lasting throughout most of the year with the exception of intermittent cold spells from November into early March, occurs there. Also, the summer (as well as the winter) temperatures are ameliorated by frequent rains. The Appalachians with ranges of about 4,000 ft. are high enough to effect the release of rain from moisture laden winds which blow from the Gulf of Mexico. The southern Appalachians have the greatest rainfall of any inland area of North America (Yearbook of Agriculture, 1941). Thus, body size is to a great extent the result of a complex interaction between environmental and specific hereditary factors, rather than a direct adaptation to a specific environmental condition as is implied by Bergmann's rule. Accordingly, the average body size of a population is a direct consequence of the climate — more accurately, of the duration and quality of the activity season. For example, wood frogs in the southern Appalachians grow to large size not necessarily because large size, *per se,* is of survival advantage but mainly because of the long, favorable season of activity which occurs in that region. Needless to say, it would be most interesting to rear northern frogs in a southern climate and southern frogs in a northern climate.

Even these explanations do not fully account for the geographic variation in size demonstrated by the wood frog. The small specimens from the Michigan area are a glaring exception and must be explained by a consideration of other factors. It is well known that variation in demes is due to the interaction of genetical and environmental factors. Accordingly, it is not surprising that some species do not attain maximum size in those regions of the range where the growing season is longer and more generally tolerable. For example, northern *Rana*

pipiens and *R. clamitans* are definitely larger than their southern counterparts.

Schmidt (1938) stated that in general, poikilothermous animals increase in size with approach to their optimum climatic conditions. Accordingly, the southern Appalachian region is closer to the optimum climatic conditions for *sylvatica* than is any other part of its geographic range. It is difficult to accept this interpretation because such a region of "optimum climatic conditions" is here restricted to the periphery of the range. Furthermore, those climatic conditions which are optimum for attainment of large body size may not be optimum for attainment of large populations. Abundance (population density), rather than body size of individual organisms, is a better criterion of biological success and hence a better criterion of optimal climatic conditions. For example, it must be conceded that, within limits, higher temperatures speed up metabolism and thus permit rapid growth; however, these same high temperatures may be detrimental or even lethal, to early developmental stages.

RELATIVE LENGTH OF LEG

The ratio of the length of the tibia (actually the tibiofibula) to the body measurement is here used as an index of the relative length of the hind legs. As a frog grows, its legs increase in length less rapidly than does its body. An example of the ontogenetic change occurring as wood frogs attain larger size is indicated by Figure 2. Mecham (1954) has shown that a similar relationship occurs in *R. clamitans*. So that this ontogenetic change would not obscure geographic varia-

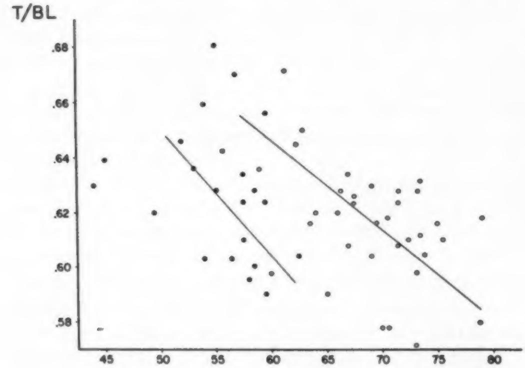

Fig. 2.—Scatter diagram showing variation in relative leg length with change in body size. Open dots represent females, solid ones males. Data are from 56 specimens collected in northeastern Georgia and adjacent parts of North and South Carolina.

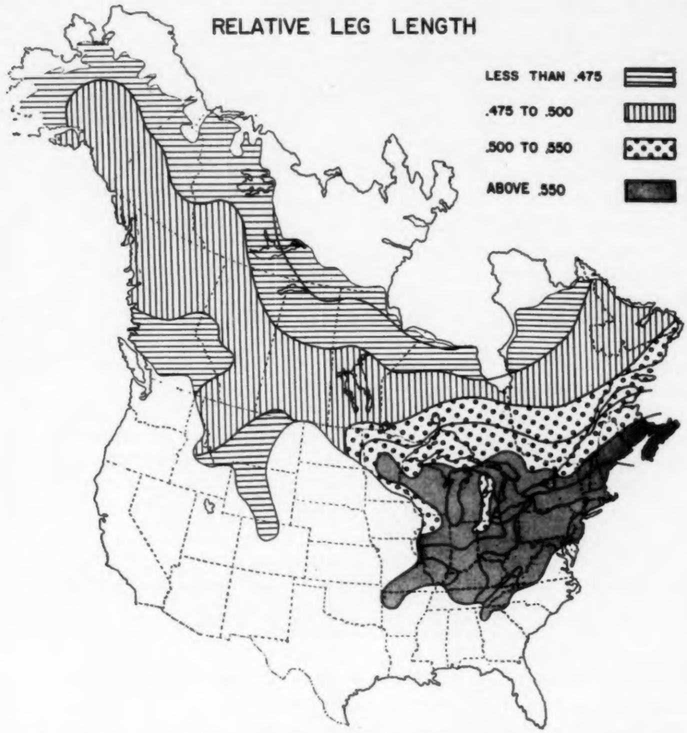

Fig. 3.—Variation in relative leg length as shown by the average ratio of the length of the tibia to that of the body. Isophenes are drawn for an interval of 0.25.

tion, adult frogs only were used. Furthermore, consideration had to be given to the ratio of the sexes in the various samples because of dimorphism — a differential rate of change shown by males and females. The mean and the standard deviation of each sample were then plotted on a map and isophenes were drawn (Fig. 3).

In the eastern half of the range of *sylvatica,* there generally exists a latitudinal gradient in relative leg length. The longest legged frogs are from the southern Appalachians; their tibias average .625 of the body measurement. The shortest legged specimens are from northern Ontario, Manitoba, and Saskatchewan; e.g., 40 specimens from Fort Severn, Ontario, average .442. Between the above mentioned groups of long and short-legged frogs, a somewhat uniform north-south gradient exists. In the Great Lakes region this pattern is

interrupted by the presence of short-legged frogs in eastern Michigan and northwestern Ohio. This condition is shown by the north-south orientation of the isophenes in that area.

In the western half of the range, the distribution of this characteristic is vastly different. There, a weak gradient exists with a poorly defined ridge, an area wherein the specimens average about .480, extending through southern Saskatchewan, central Alberta, northern British Columbia, southern Yukon Territory, and southern Alaska. To the north and south of this ridge, the populations average about .470. It is especially interesting to note that specimens from the Wyoming-Colorado area average even less, about .460. This is in marked contrast to the situation in the southeastern part of the range. It seems obvious that long legs are not an adaptation to rough terrain *per se*.

The tendency for the relative size of bodily extremities to decrease northward (Allen's rule) is substantiated by this study of the wood frog only in a very vague way. In those regions where low temperatures and short seasons of activity prevail (as in the northern and western parts of the range) there is generally a reduction in the relative length of the hind legs. Possibly short legs are an adaptation for surviving arctic and subarctic winters; however, very little is known about hibernation of cold-blooded vertebrates in these regions. Turner (1886) reported that the Alaska blackfish, *Dallia pectoralis,* can survive freezing each winter in solid ice. Wynne-Edwards (1952) indicated that Turner's report needs corroboration and further stated that few or no cold-blooded vertebrates can survive the arctic winter except in fluid water. This viewpoint was confirmed by Scholander *et al.* (1953). Their experiments showed that *Dallia* could not be anywhere near completely frozen and still survive. Darlington (1957) stated that perhaps northern amphibians hibernate under water deep enough to protect them from extreme cold. On the other hand, it is well established that shortness of the legs is correlated with burrowing and elongation of the limbs with more active habits (Schmidt, 1938). Accordingly, once warm weather releases northern wood frogs from their hibernacula, they breed and move to feeding areas. Here they probably depend upon their ability to burrow into niches where they can withstand the intermittent, but frequent, periods of cold weather, which occur throughout their activity season.

There is a general correlation between the distribution of isophenes for body size and those for relative leg length. Both show a well defined gradient in the east and a poorly developed one in the west. The frogs which inhabit the southern Appalachians are very large in body size and have exceptionally long legs. This characteristic is contrary to the general tendency (shown in Fig. 2) for the hind legs to become relatively shorter as a frog grows in length. Hence long-leggedness appears to be a paedomorphic characteristic. Along the west side of the Appalachians there is a very steep gradient in body size. The isophenes for relative leg length show their steepest gradient in the Ohio-eastern Michigan-southern Ontario-New York area and

coincide somewhat with those for body size. The main areas of discord are in the southern part of the Appalachians where there is a steeper gradient for body size and in the eastern part of Canada where the gradient for leg length is much greater than that for body length. The outstanding feature in the western part of the range is that the frogs from Colorado-Wyoming are somewhat large in body size but relatively small in leg length. Their legs are about the same relative size or smaller than those of frogs from farther north. This conspicuous difference between the relative leg lengths of southeastern and southwestern wood frogs may be attributed to differences in rainfall and humidity. As already mentioned, large frogs have less surface area per unit of weight, hence they lose relatively less water through evaporation in a given period of time. However, with regard to the large frogs from the southern Appalachians, some of this advantage is lost because they have relatively long legs. On the other hand, the increase in surface afforded by their longer legs can be partly offset by behavior — the legs are pulled in, close to the body, when the frogs are forced to become inactive, as during times of low humidity. However, the southern Appalachian area is a relatively moist region. About four times as much rain falls there from April to September, as occurs in the Rockies (Yearbook of Agriculture, 1941). Thus short legs may be of possible advantage in regions of low humidity and low temperature, such as those occurring in high latitudes and at high elevations. It is possible that humidity is the factor which upsets Bergmann's and Allen's rules in the western part of the range, and furthermore, accentuates them in the east. However, if this is true, then how does one explain the outstandingly small size and short-leggedness of the frogs in the Great Lakes region?

SEXUAL DIMORPHISM IN BODY SIZE

For those samples in which adequate representation of both sexes were available, the average body size of the females was divided by that of the males. The values (ratios) thus obtained were plotted and isophenes drawn (Fig. 4). In general, sexual dimorphism in body size is greater in the southern part of the range than farther north. The greatest dimorphism occurs in specimens from the southern Appalachians and the Ozarks. Specimens from the Georgia-North Carolina region have an average ratio of 1.21. These greatly dimorphic frogs extend northward through the Appalachians to New England and to southern Ontario. Specimens from Colorado-Wyoming also have relatively high dimorphic indices, however, they average only 1.16. The least dimorphism occurs in the Northwest Territories and in northwestern Alberta where ratios as low as 1.02 occur.

The strongest gradient is located in the southeastern part of the range. A well developed gradient is present in the west; however, over the middle and northeastern parts of the range the gradient is very weak. It is noteworthy that specimens from northern Michigan have

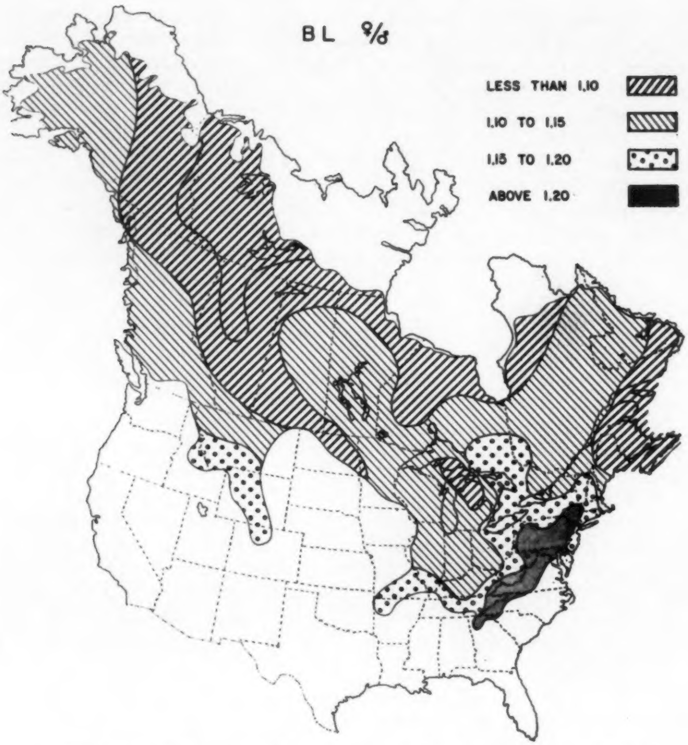

Fig. 4.—Sexual dimorphism as shown by the average ratio of the body length of females to that of males.

a low index of sexual dimorphism. Furthermore, the isophenal pattern for sexual dimorphism and that for body size show much general agreement. With an increase in the average body size, there is a greater difference between the sexes. The selective advantage of sexual dimorphism in body size is at present not enough understood to warrant a discussion of the significance of its geographic variation.

MIDDORSAL WHITE LINE

The middorsal white line is a prominent feature of many northern wood frogs (Figs. 8, 9). In general, it extends from the tip of the snout over the dorsum and onto the posterior surface of the thigh, shank, and foot. It is well developed in small as well as adult frogs, hence it does not change ontogenetically. Furthermore, this trait is not

sex-linked. It is characteristic of more than half of the specimens from northern Quebec, Manitoba, northern Saskatchewan, the Northwest Territories, the Yukon, most of Alaska, southern British Columbia, Alberta and the Wyoming-Colorado area (Fig. 5). In the southeastern part of the range, Labrador southwestward into Arkansas, the middorsal white stripe is absent. In general, it is absent on specimens from the Great Lakes region, however, some notable exceptions occur. It is present on about eight percent of the specimens from Keweenaw County, Michigan and the adjacent northeastern part of Wisconsin; and on two specimens from Jo Daviess County, Illinois; one from Miami County and one from Warrick County, Indiana; and one from Hocking County, Ohio. Undoubtedly it also occurs sporadically in other areas. All specimens from Colorado-Wyoming and from the region of Fortymile, Yukon Territory possess the middorsal stripe.

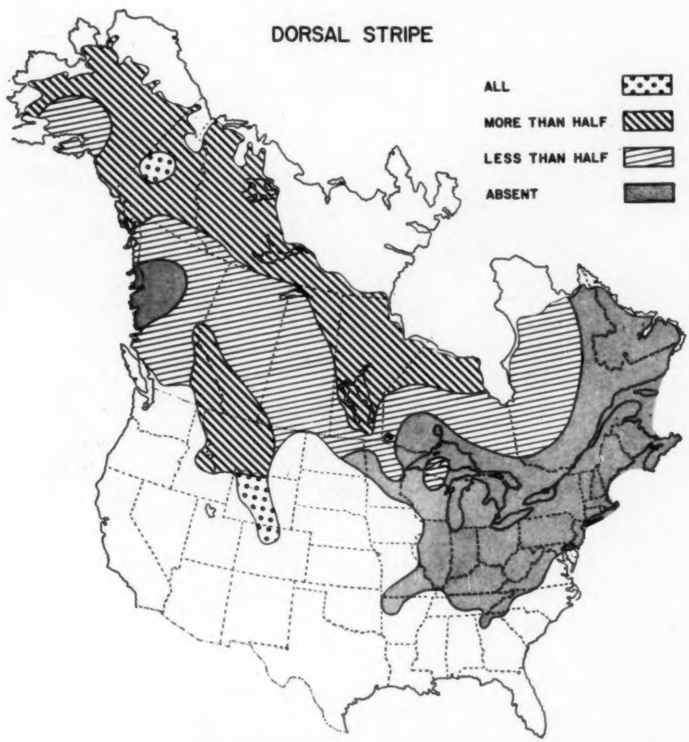

Fig. 5.—The distribution of the middorsal white stripe. See text for exceptions which occur in area designated "absent."

In sharp contrast, frogs from western British Columbia lack the mid-dorsal white stripe.

It was interesting to note that among the specimens examined, the white stripe was either fully present or entirely absent. It is very likely that the stripe is due to a single gene. This interpretation is in accord with the few analyses that have been made of inheritance in amphibians. These studies have demonstrated that major changes in color patterns are often due to single genes (Moore, 1942, 1943; Goin, 1947; Volpe, 1955).

TIBIAL BARS

The number and intensity of the transverse markings (bars) on the dorsal surface of the shank varies among wood frogs. In general, two or three bars are present; however, the number varies from none to

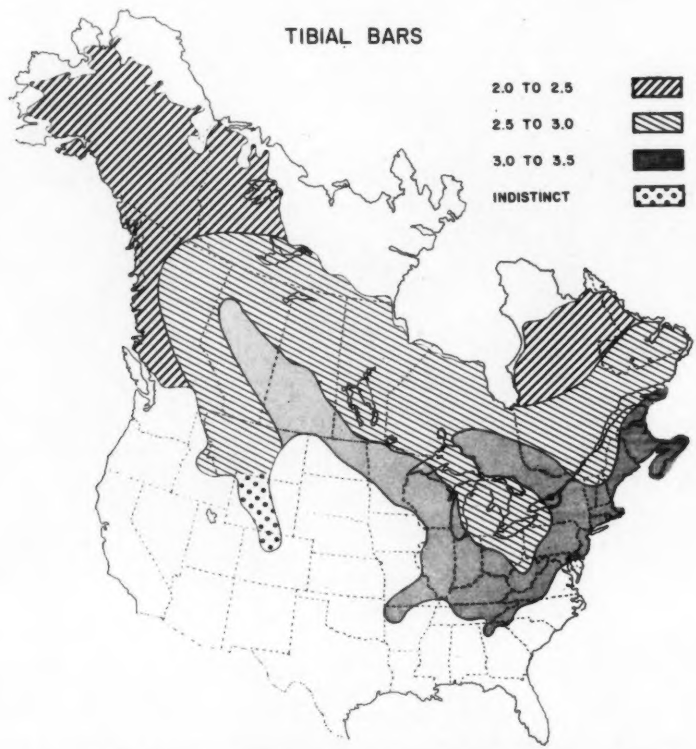

Fig. 6.—Variation in the number of transverse markings on the shank.

seven (Figs. 8-13). In all parts of the range there is much variation; this prompted a consideration of the averages and standard deviations for specimens from the different areas represented. These values were plotted and isophenes (arbitrarily selected) were constructed for 2.5 and 3.0 tibial bars per leg (Fig. 6). Specimens from the southeastern part of the range have the most bars and these are also the most regular and distinct. Specimens from Alaska, the Yukon Territory, and adjacent British Columbia, together with those from northern Quebec and Colorado-Wyoming have the least number of bars, they average less than 2.5 per leg. Furthermore, they have the most irregular and most indistinct bars. For example, only about 20 percent of the Colorado-Wyoming specimens have distinct bars, while about 25 percent lack bars entirely. Again there is a tendency for southern populations to differ from northern ones. In the eastern part of the range the trend for southern frogs to have more bars than do more northern ones is quite apparent, while in the western part of the range it is very weak or absent — like so many of the other characters studied. Once more, the frogs of the Great Lakes region are salient because of their similarity to more northern populations.

OTHER MARKINGS

All specimens examined possessed a prominent pectoral spot on each side of the body. This persistent marking is also present in other species, namely, *R. pipiens* and *R. palustris*.

A well-developed dark patch of color extends from the tip of the snout through the eye and onto the side of the head of all *sylvatica* examined. It also occurs in several other species of *Rana,* mostly European ones. Cott (1940) noted that "few natural objects possess greater inherent conspicuousness than the vertebrate eye." He stated that such a marking, as the eye mask, camouflages the eye and classified it as a "coincident disruptive pattern."

No attempt was made to classify specimens as to the darkness or lightness of their dorsal patterns; however, it was obvious that the darkest specimens were those from Maine (Figs. 12, 14). Gloger's rule that races inhabiting warm or moist regions tend to be more melanistic than those in cool or arid areas does not add meaning to our observations. Maine is far from being the warmest or the most moist region occupied by *sylvatica*. Furthermore, the frogs from the cool and dry parts of Alberta and British Columbia are not outstandingly light in body color.

The more conspicuous markings of western and especially northern wood frogs, as compared to southeastern ones, may be attributed to their more diurnal activity. This is the result of (1) the long daylight period in the summer season and (2) rapid nocturnal radiation of heat from the earth. If frogs are to survive in a region where the season of favorable temperature is greatly reduced, their activities must be adjusted to utilize every opportunity for feeding, growth, etc. They

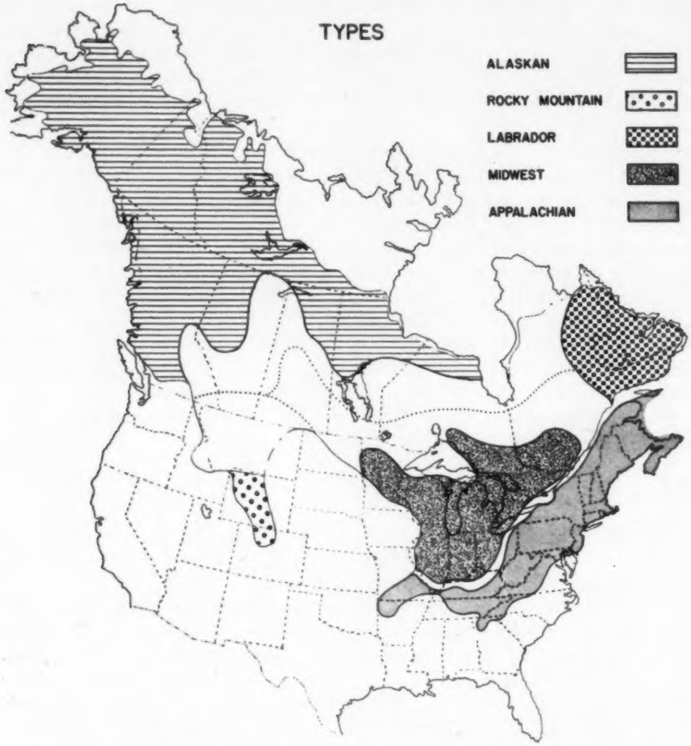

Fig. 7.—Distribution of the phenotypes. The zone of intergradation is shown by the unmarked area. The dotted line indicates where the adjacent type is predominant.

are forced to become active during the daylight hours when warming via insolation occurs and to seek refuge when cooling takes place, as in the evening. This is in marked contrast to the situation in the southern part of the range where the season of activity is of longer duration and, except at its beginning and end, not interrupted daily by low temperature. This greater diurnalism on the part of northern frogs increases the selective pressure on coloration and markings. In these frogs the general background color, as well as the ability to effect color changes, is very important in heat economy. Furthermore, the vivid disruptive coloration of northern wood frogs, as shown by markings such as the middorsal stripe, the dark eye patch, dorsolateral fold markings, tibial bars and pectoral spot, is outstandingly well developed. Presumably it functions mainly to provide concealment from predators.

PHENOTYPES

After examining many large series of wood frogs, we noted that they could easily be divided into groups according to visible characters: general coloration, markings, size, appearance, etc. Since these characters are the results of interaction between genetic and environmental factors, the various groups of frogs are referred to as "phenotypes" or simply as "types." Five discrete groups were recognized: Rocky Mountain, Alaskan, Labrador, Appalachian, and Midwest. Representative specimens were selected for each type and these were set aside as references. These typical specimens, shown in the photographs included in this study, were used as standards by which all other specimens were grouped. In classifying specimens, we did not consider the locality of collection. The geographic distribution of these types is presented in Figure 7.

The wood frogs occurring in Colorado, Wyoming, and probably in Montana, constitute the most obvious type (Fig. 8). It is referred to as the Rocky Mountain type. The background color is light tan dorsally, becoming clear and whitish on the lower sides of the body and in the groin. The dorsolateral folds are broad, flat, and heavily pigmented. The dorsal pattern is striking. All specimens have a broad middorsal light colored stripe, bordered on each side by a dark tan or brownish region. The lateral portion of the dorsum is light tan, this color extends from the brownish dorsal region to the medial edge of the dorsolateral fold. In contrast, the lateral edge of each fold is darkly pigmented. It is almost as dark as the brownish pigment bordering the middorsal light stripe. The tibial markings are poorly developed. They are distinct as bars in only 20 percent of the specimens and are absent in about 25 percent. On most specimens they are represented by very indistinct and irregular spots. Furthermore, the Rocky Mountain type is readily distinguishable from more northerly populations because of its relatively longer hind legs.

The Alaskan type occupies the northwestern third of the range of *sylvatica* and is the most widely distributed type. It is similar to the

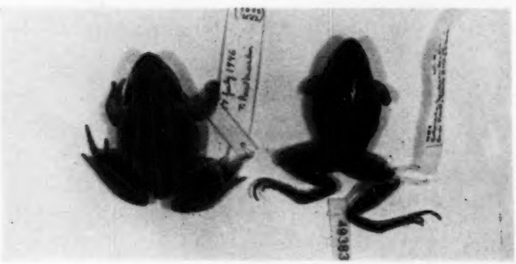

Fig. 8.—Rocky Mountain type, females, from Jackson County, Colorado (T. P. Maslin No. 2120, left; Univ. Calif. Mus. Zool. No. 49383, right).

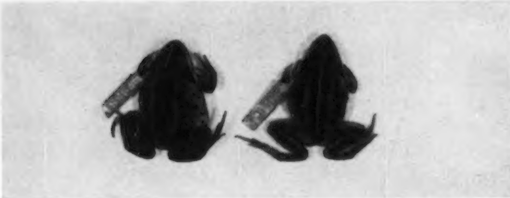

Fig. 9.—Alaskan type, females, from Kobuk, Alaska (Univ. Mich. Mus. Zool. No. 98815V and FF).

Rocky Mountain type, but in general, is darker and somewhat smaller (Fig. 9). The dorsum is brown with a grayish or bluish tint. The groin and lower side of the body possess dark brown markings on a bluish-white background. As in the Rocky Mountain type, there is a uniform reticulated zone between the dorsal and ventral pigments. The striking dorsal pattern described for the Rocky Mountain type is only infrequently encountered, and even then, it is never as pronounced. Only about half of the specimens have a middorsal light stripe on the dorsum. The pigment along the dorsolateral folds and on the dorsum is black, thus the dorsolateral folds are more heavily pigmented than are those of the Rocky Mountain type. The folds of the Alaskan type are similar to those of the Rocky Mountain, the chief difference being that they are smaller, in fact, almost nonexistent in some specimens.

The Alaskan and Rocky Mountain specimens have larger lateral markings than other *sylvatica*. The Alaskan type has a greater number of lateral markings than any other type. The lateral spots of all *sylvatica* have warts associated with them. These warts are best developed in the Alaskan and Rocky Mountain specimens and least developed in the Appalachian type. The hind legs of the Alaskan type, like those of the Rocky Mountain, Labrador, and Midwest types, are

Fig. 10.—Labrador type, female, Carn. Mus. No. 18040, on left, from Hamilton Inlet, Labrador; males, Univ. Mich. Mus. Zool. No. 2117 and 2118, from Northwest River (village), Labrador.

smooth skinned. All *sylvatica* have darker pigmentation on the lateral side of the dorsolateral folds than on the median side; however, this difference is best shown in the Rocky Mountain and Alaskan types.

The Labrador type occurs in Labrador and possibly in eastern Quebec. It is suggestive of the Alaskan and Appalachian types and to a great extent, the Midwest type, hence it is poorly defined (Fig. 10). Most individuals are remarkably uniform in coloration: there is a lack of contrast in pigmentation on the entire animal. The general ground color is dark in most specimens; however, in some it is light brown. The dorsal coloration of a few specimens suggests the dusky middorsal area of the Midwest type. Most specimens have mottled sides and thus suggest the Alaskan type; however, in general their lateral spots are smaller and fewer than those of the Alaskan type. The dorsolateral folds are weak and fairly broad, thus intermediate between the Alaskan and the Midwest and Appalachian types. None possesses a middorsal white line. There are only a few spots or flecks on the posterior part of the dorsum. The skin of the hind legs is smooth. More specimens from the eastern Quebec-Labrador area are needed before this population can be adequately classified.

The Appalachian type occurs in the southern part of the range in Arkansas, southern Kentucky, Tennessee, eastern Ohio and south of Lake Ontario and the St. Lawrence River. This type has the largest body size and proportionally the longest legs. Its body color is chestnut brown and is more reddish than the Midwest type (see Fig. 11).

The dorsolateral markings (spots) are black or very dark brown. The dusky middorsal area, so frequently found in the Midwest type, is absent. There is a gradual transition from the light color of the venter to the darker dorsal coloration; however, the dorsal pigments

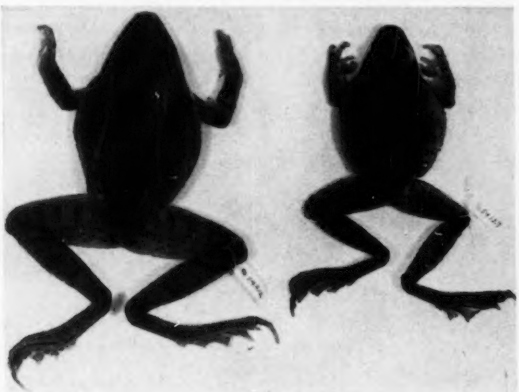

Fig. 11.—Appalachian type, female on left Charleston Mus. No. 54.9.12; male, Charleston Mus. No. 54.32.9, both from Cherokee County, North Carolina.

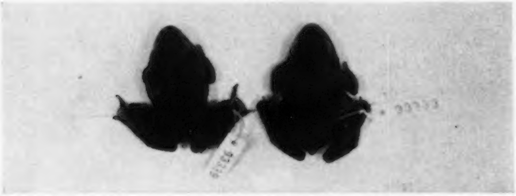

Fig. 12.—Maine specimens, female on right, both from Penobscot County, Maine, Univ. Mich. Mus. Zool. No. 93339.

extend far over the sides of the body, making this type even more dark-sided than the Alaskan type. Of all the types, the Appalachian has the most rugose hind legs. Specimens from Maine are outstanding because of the comparatively abrupt transition from the dark chestnut of the dorsum to the yellowish-white of the venter, thus providing a conspicuous contrast. Then too, the ventral markings are conspicuous because of the strong contrast to the light background color. They are as dark as the dorsal coloration but not as intense. Except for their small body size, shorter and less rugose legs, the Maine specimens (Figs. 12, 14) are similar to those occurring farther south and are best classified as the Appalachian type.

In spite of considerable seasonal variation, sexual dimorphism, as shown by enlargement of the "thumb," forearm, and webbing between the toes, is very pronounced in the Appalachian and Labrador types; it is less pronounced in the Midwest type, and least in the Rocky Mountain and Alaskan types. Another difference is that the Appalachian specimens are more blunt nosed than other wood frogs; the Rocky Mountain, Alaskan, and Labrador types are sharp nosed, while the Midwest type is intermediate.

The Midwest type (Fig. 13) occurs in the midwestern states and in southern Ontario and Quebec. The ground color of these phenotypically distinct populations is browner than that of the Alaskan and

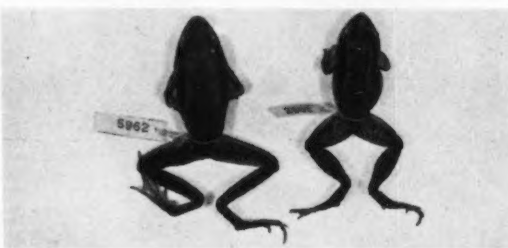

Fig. 13.—Midwest type, female on left, Chicago Acad. Sci. No. 5962, from Porter County, Indiana; male, Chicago Acad. Sci. No. 2805, from LaPorte County, Indiana.

Rocky Mountain types. Actually, it is suggestive of the Appalachian type. The dorsal and lateral markings are dark brown, smaller and less numerous and more diffuse than those of the Alaskan type. Commonly there is a dusky middorsal area which becomes lighter toward the dorsolateral folds. Some specimens have a middorsal light line. A reticulated or flecked pattern on the sides of the body makes a gradual change from ventral to dorsal pigmentation. In general, specimens are light-sided, the dorsal pigmentation does not extend far onto the sides of the body. The dorsolateral folds are narrow and low, the skin on the hind legs is smooth.

To the north, the Midwest type intergrades with the Alaskan type and to the northwest, with the Rocky Mountain type. The zone of intergradation between these groups is very broad, especially in comparison to the very narrow belt which lies between the Midwest and Appalachian types. This is particularly interesting because the Midwest type bears strong similarity to the Appalachian type.

GENERAL DISCUSSION

One of the outstanding facts, revealed by this study, is the distinctiveness of frogs from the Great Lakes region, especially the Michigan area. Their small body size, small relative leg length, reduced sexual dimorphism in body size, small number of tibial bars, and the scattered presence of individuals with a middorsal white stripe — in all these features they are strikingly similar to more northern frogs. This is somewhat surprising because they are classified as the Midwest type, a group which is highly similar to the Appalachian type. It should be noted that the phenotypic designations are largely subjective and are based heavily on coloration and markings and to a lesser extent on body size and proportions of parts. This apparent discrepancy is

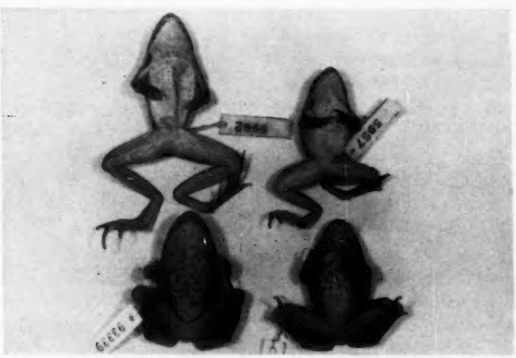

Fig. 14.—Ventral view of Midwest type (upper pair, female on left) and specimens from Maine (lower pair, female on left).

brought about because meristic characters are not readily evident upon visual examination of specimens. Accordingly the impression of the frog as to type is not borne out completely in measurable quantities.

As explanation of the presence of these northern characters in the Great Lakes area, let us first inspect the possible effects of the most outstanding environmental factor, the climate of that region. Records show that the Great Lakes greatly influence the climate of the adjacent area, especially the eastern shores (Kendrew, 1953). By their retention of the summer heat, the lakes warm the surrounding area, starting in October and continuing until February; a corresponding cooling effect occurs in late spring and early summer. However, correlation of this ameliorating effect with data on the activity season of wood frogs does not convincingly account for the distinctiveness of these frogs.

The most plausible explanation for the presence of northern characteristics among these wood frogs and for the geographic variation of this species in general, is that afforded by an analysis of their history. A brief synopsis follows. Ranids originated in the main part of the Old World tropics; from there the genus *Rana* has spread throughout the northern part of the world (Darlington, 1948, 1957). Simpson (1947) has presented evidence that extensive exchanges of land vertebrates, especially mammals, occurred between Eurasia and North America at various times from the early Eocene to the Pleistocene. In general there was more movement from Eurasia to North America than in the reverse direction. Presumably the progenitors of *sylvatica* came to Alaska via the Bering Strait during one of these exchanges. It has long been recognized that *sylvatica* is closely related to *temporaria* of Europe and Asia (Cope, 1875; Boulenger, 1920). So strikingly similar are these frogs that Cope first referred to *sylvatica* as a subspecies of *temporaria*. It is logical to assume that since the climate was favorable for migration from Asia, the climatic conditions in North America were also favorable for dispersion of wood frogs. Thus from Alaska they spread eastward and southward.

Just when wood frogs came to America is not too important to an understanding of their present-day variation, but the events which have occurred since the last continental glacier began to withdraw — only about 10,000 years ago (Libby, 1956) — are of paramount importance. The mode of origin of the Wisconsin ice sheets of North America and their migrations and general history are known with a surprising amount of detail (See Flint, 1947.).

Associated with the gradual cooling of northern climates during the last glacial period, there was a southward shifting of northern vegetation zones (Barghoorn, 1953). Considerable information about the climatic and biogeographic conditions has been derived from pollen analyses of peat bogs. Dillon (1956) has integrated much of the geological, climatological, and biological data pertaining to glaciation. He depicted the development of the Wisconsin glaciation by showing the distribution of the ice sheets at various stages. On the

same maps he also showed the distribution of *Picea glauca* (white spruce). As the glaciers moved southward, so did *P. glauca*. On the map showing the Wisconsin maximum, the distribution of *P. glauca* is confined to the United States and is divided into two segments, a western and an eastern one. The gap between these segments occurred in the region of the Great Plains Province. Presumably it was due to unfavorable climatic conditions created by the Rockies, namely, adiabatic warming of air already deprived of its moisture. In view of the fact that the present distribution of *sylvatica* generally approximates that of *P. glauca,* it follows that during the Wisconsin glaciation, these species very likely had somewhat similar distributions. More pertinently, the same factors which brought about a division of the range of *P. glauca* probably effected a break in the range of *sylvatica.*

With the onset of deglaciation, the western segment of the wood frog population was in a more favorable position to move northward. There are several facts (Flint, 1947) which support this conclusion. The Cordilleran Ice Sheet was thick but did not extend very far to the east of the Rockies. The Laurentide Ice Sheet was very thick in the southeastern part of its range but was thin in the Great Plains section of Canada. This thinness was due to the long uphill slope of the plains traversed by the ice sheet as it approached the Rockies and secondly, to the absence in that region of moisture-bearing winds. It is also significant that according to Flint, "The presence in east-central North America of an extensive system of capacious valleys, dating from preglacial time but enlarged by glacial scour, and depressed regionally under the weight of the ice sheet, led to the development of the magnificent sequence of glacial lakes whose successors are the modern Great Lakes. The earlier-formed lakes were ponded between high ground on the south, and the ice-sheet margin on the north. Later, as the ice melted away, and the land, relieved of the weight of the ice, slowly rose, the lakes fell to lower levels and by gradual stages became confined to the basins they occupy today." Flint further noted that after west-central Canada had been deglaciated, resistance of the ice to further wastage became more stubborn. "It is probable that the ice disappeared from the Hudson Bay region while persisting over the Quebec highlands and the Labrador mountains." Thus the wood frogs in the eastern part of the United States moved northward at a somewhat later date than did those in the west. As a consequence, the frogs from the west moved into the central part of the continent earlier than those from the southeast and into the the northeastern part at about the same time as did the southeastern frogs.

Pollen profiles indicate that in the eastern and midwestern parts of the United States a warm, moist period soon followed the retreat of the glaciers. During this period, conditions (see Smith, 1957; Thomas, 1951; Conant *et al.,* 1945) were favorable for wood frogs to move into that region. These frogs came mainly from the northwest (the (Alberta-Saskatchewan area) but also from the Appalachian region. Thus in the Midwest and Great Lakes area the populations, isolated

during the apogee of glaciation, met and mixed. Later (circa 4,000 to 6,000 years ago) a warm, dry climate prevailed and the prairie region, located leeward of the Rockies, extended eastward south of the Great Lakes and almost to the Atlantic Coast. At its maximum this prairie peninsula must have been an impassible barrier to wood frogs. In this way the populations of the Southeast were isolated from those to the north of the prairie peninsula; furthermore, relict colonies, such as the Kansas population, were formed. During this period of isolation, gene flow continued to occur in the region north of the peninsula thus accounting for much "swamping" of southern characters, even in populations in the eastern part of Canada. With the subsequent return of a cooler, moister climate to eastern North America the grassland was replaced by a mesic forest. Now conditions were once more favorable for gene flow from the Southeast and the setting was laid for the formation of the various races (types) which now exist.

The Rocky Mountain type was derived from the western segment of the species population which existed during the Wisconsin maximum. It occupies the same general area as did its ancestral stock. As already indicated, the western segment of the population gave rise to the stock which early migrated northward into west-central Canada when deglaciation got under way. From this area, wood frogs later spread into Alaska and into British Columbia, also they dispersed eastward and southeastward as the receding glaciers permitted. Thus the Alaskan type was formed. It is outstanding for its great dispersal and extensive gene flow as shown by the weak clinal gradients over the area it occupies.

The eastern segment of the species population which existed during the Wisconsin maximum survived in the southeastern part of the continent and gave rise to the Appalachian type. The "cantabrigensis" stock was derived from the mixing of the Appalachian and Alaskan populations. This was made possible by the withdrawal of the glaciers. With the subsequent development of the prairie peninsula and the cessation of gene flow from the Southeast, this stock developed a decided Alaskan aspect. Later with the passing of the prairie peninsula and the re-establishment of gene flow from the Appalachian region, this stock was again modified and at the present time it is still being modified by the inflow of southern genes. The western portion of the "cantabrigensis" stock represents the Midwest type, while the eastern portion, which was less isolated from southern genes (because of migration around the eastern limit of the prairie peninsula), but more isolated from northern genes (because of distance), formed the poorly-defined Labrador type.

It is unequivocal that the establishment of the subspecies concept and the adoption of trinomial nomenclature have played a major role in promoting our understanding of the part that geography plays in speciation (Rensch, 1934). However, it must also be conceded that the trinomial has become a hindrance to our understanding of infraspecific relationships. Its shortcomings have been outlined by Wilson

and Brown (1953), Brown and Wilson (1954), Borgmeier (1957), and others, and will not be repeated here.

Furthermore, we think that Bergmann's, Allen's, and Gloger's rules have been greatly overemphasized. They have promoted the investigation of ecological factors, but in the meantime, have impeded our understanding of geographic variation about as much as has the trinomial. These vague generalities are no substitute for knowledge of (1) the genetical and physiological mechanisms which produce ecological adaptation and (2) the influence of migration (gene flow) on the genetic composition of local populations. Among the most meaningful studies of the role that ecological factors play in altering morphology, physiology, development, and activity of salientians are those of Moore (1944, 1949, 1949a) and Thorson (1955, 1956). These experimental analyses provide exemplary starting points for future studies which attempt to clarify geographic variation. Also noteworthy is the excellent work of Dowdeswell, Fisher, and Ford (1949), which stresses the importance of the role that seemingly minor ecological and other barriers play in micro-evolution, and that of Dowdeswell and Ford (1952), and Ford (1954), which indicate that obvious environmental diversity may not lead to conspicuous morphological differentiation unless isolation of populations occurs.

SUMMARY AND CONCLUSIONS

The geographic range of *Rana sylvatica* is large; it covers approximately four million square miles and extends from the northern limit of wooded country in Alaska and Canada south to Georgia and Arkansas, northward east of the Mississippi River to Minnesota, and westward in North Dakota to the Pacific. In the Rockies, scattered populations occur southward to Colorado. The availability of favorable temperature and habitat limits the distribution of wood frogs. This species is outstanding because of its tolerance of cold temperature and a short annual activity season. It ranges farther north than any other cold-blooded tetrapod in the Western Hemisphere.

From a superficial examination of the 2,801 specimens assembled for this study, it was evident that considerable variation existed. Our objective was to ascertain the nature of this variation and then to describe and interpret it. To attain this objective we used two approaches. The first involved the analysis of single, measurable characteristics, such as body size, relative leg length, etc. Each feature was shown on a map where isophenes depicted its geographic distribution. The orientation and spacing of these isophenes was interpreted to show in part the general direction and rate of dispersion, hence gene flow within the species population. Most gene flow is parallel to the isophenes, especially in those regions where the isophenic gradient is steep (as shown by the closeness of isophenes). In regions of weak gradient, extensive gene flow occurs, even in a direction which crosses an isophene; however, even here the rate of gene flow is greatest in the

general direction indicated by the orientation of the isophenes. Especially noteworthy among these data are the relative genetic isolation of the frogs in the southeastern part of the range and the extensive gene flow over the other parts, particularly the western.

The largest wood frogs occur in the southern Appalachians. To the north of this area body size decreases gradually. There is a steep gradient in size along the west side of the Appalachians. The smallest frogs inhabit northern Manitoba, northern Saskatchewan, and the adjacent part of the Northwest Territory. A weak gradient extends over the western half of the range.

Ontogenetically, relative leg length decreases with an increase in body size. The longest relative leg lengths occur in the southern Appalachians, where the average is about 62 percent of the snout-vent measurement. The shortest legged specimens are from northern Ontario, Manitoba, and Saskatchewan; they average about 44 percent. A somewhat uniform north-south gradient occurs in the eastern part of the range, whereas in the west a weak gradient occurs, and in the southwest the gradient is reversed.

Sexual dimorphism in body size is greatest in specimens from the southern Appalachians; specimens from Georgia-North Carolina have a ratio of 1.21 (females/males). The least dimorphism occurs in the Northwest Territories and northwest Alberta where ratios are as low as 1.02. In contrast to other characters, a moderately steep gradient occurs in the western part of the range. Frogs from the southern Rockies have an average ratio of 1.16.

A middorsal white line is present on all specimens from the southern Rockies and from some areas in the Yukon Territory. In general, most specimens from Alaska and northern Canada have the middorsal line, whereas less than half of those from central Canada possess this feature, and those from the southeastern part of the range lack this marking.

Wood frogs generally have two or three tibial markings; however, the number varies from none to seven. Northern frogs average fewer markings than do the southern ones; however, those from the southern Rockies have the most irregular and most indistinct bars. Furthermore, about 25 percent of the specimens from that area lack bars. All wood frogs possess a prominent pectoral dark spot on each side of the body and a well developed eye mask. Specimens from Maine are outstanding because of their dark dorsal coloration whereas those from the Michigan area are unique because of their striking similarity to more northern frogs.

After we had measured and examined representative materials from different parts of the range of this species we resorted to a second approach. This consisted of a comparative evaluation of phenotypic characteristics. The composite features of individual specimens were now used. Because no conventional units are used to evaluate the composite variation of an entire organism, this method is largely subjective. We early noticed that the specimens could readily be grouped. Stand-

ards (type or reference specimens) were selected for each group or phenotype, and all specimens available were classified in accordance with these standards. Five discrete groups were noted: ***Rocky Mountain,*** from the southern Rockies; ***Alaskan,*** the northern third of the range; ***Labrador,*** eastern Canada; ***Appalachian,*** eastern United States and the Ozarks; and ***Midwest,*** from the Great Lakes region.

This method closely approximates that of modern taxonomists wherein infraspecific variation is expressed in terms of subspecies, each of which is represented by various type specimens. In view of the provincial way that many subspecies have been studied and described, it is somewhat surprising that there is some correlation between the phenotypes and the formally established subspecies. For example, the Alaskan type can be construed to be the equivalent of *latiremis,* the Rocky Mountain is unnamed, the Labrador type (poorly defined and represented by relatively few specimens) represents the eastern part of the *cantabrigensis* stock, the Midwest type represents the main body of the *cantabrigensis* stock, while the Appalachian type can be interpreted to be *sylvatica. R. s. cherokiana* is not distinct, it represents the populations in the southern Appalachians which are somewhat larger in body size, but nevertheless very similar to populations from the more northern part of the Appalachians.

In spite of the general conformity of subspecies and phenotypes, we think that formal scientific names are not warranted. Much confusion results if adherence to formal subspecies is maintained. We think that all wood frogs should be referred to simply as *Rana sylvatica.* On the other hand, we are of the opinion that the establishment of the various phenotypes has very definitely aided us in understanding the geographic variation of this species. The grouping of the specimens into phenotypes seemed a natural consequence of our efforts to comprehend their variation.

The trinomen has passed through its stages of being useful. The task of justifying the retention of the subspecies as a formal taxonomic category rests with those who wish to retain it. Studies of infraspecific variation do not necessarily reveal "evolution at work" but more accurately they survey the general status of variation exhibited by the various populations. The presence of geographic variation does not inevitably imply species formation.

Furthermore, the so-called ecological rules (Bergmann's, Allen's, and Gloger's) have impeded the understanding of geographic variation about as much as has the trinomial. They are no substitute for an understanding of (1) the genetical and physiological mechanisms which produce ecological adaptation and (2) the influence of migration (dispersion) on the genetic composition of local populations.

The most plausible explanation of the geographic variation of this species is that afforded by knowledge of the Wisconsin glaciation. The migrations of wood frogs are closely associated with the distribution of favorable habitat resulting from the activity of glaciers.

NUMBER AND DISTRIBUTION OF SPECIMENS EXAMINED

UNITED STATES

ARKANSAS—*Crawford Co.,* Bidville (3); *Franklin Co.,* Ozark, near Arkansas River (1); Madison Co., 11 mi. N. of Kingston (1); *Washington Co.,* Devil's Den State Park (1), Winslow (2).

COLORADO—*Jackson Co.,* 2.5 mi. E Rabbit Ears Peak (5), 5 mi. ESE Rabbit Ears Peak (8), 8 mi. W Coalmont and 1 mi. N Sawmill Creek (1), Rand (2).

GEORGIA—*Fannin Co.,* Rock Creek near Rock Creek Lake (5), Rock Creek Refuge, trout rearing pools (8), between Hawk Mountain and Mill Creek Fish Hatchery (5), Springer Mountain (4); *Towns Co.,* 4 mi. from Ga. route 75 along Ga. route 64 (1). 7 mi. S Hiawassee (1); *Rabun Co.,* Lake Burton Dam (1); *Union Co.,* Tocoa Experiment Station (5).

ILLINOIS—*Champaign Co.,* Homer (1); *Clark Co.,* Rocky Branch (1); *Coles Co.,* Fox Ridge State Park (16), Charleston (1), others (9); *Effingham Co.,* 3 mi. NE Mason (1); *Jackson Co.,* Murphyboro, Rattlesnake Canyon (4); *Jo Daviess Co.,* 6 mi. NW Galena (4); *Lake Co.,* Deerfield (20); *Monroe Co.,* 2 mi. E Valmeyer (1); *Richland Co.,* (1); *Vermilion Co.,* (1).

INDIANA—*Allen Co.,* 4 mi. NW Arcola (1); *Cass Co.,* Mud Creek (2), Hoover (2); *Crawford Co.,* 2 mi. N Sulphur (2); *Fayette Co.,* (3); *Fountain Co.,* Portland Arch (1); *Jackson Co.,* Crothersville (1); *Jefferson Co.,* Clifty State Park (4); *Kosciusko Co.,* Lake Winona (2); *LaGrange Co.,* Pigeon River (1); *LaPorte Co.,* Smith (9); *Marion Co.,* Indianapolis (1); *Miami Co.,* 2 mi. W Peru (8); *Noble Co.,* 2 mi. NE Wilmot (1); *Owen Co.,* McCormicks Creek State Park (1); *Porter Co.,* Dune Acres (4), Wilson (6), Chesterton, Coffee Creek (1); *St. Joseph Co.,* North Liberty (3); *Starke Co.,* 5 mi. W Culver (1), 4 mi. S Knox (3); *Steuben Co.,* Jamestown Township, South Lake George (3); *Vanderberg Co.,* Perry (2); *Warrick Co.,* (1); *Washington Co.,* Muscatatuck Bottoms (1).

KANSAS—*Lyons Co.,* 15 mi. S Plymouth (1).

KENTUCKY—*Adair Co.,* Coburg (1); *Bell Co.,* near Harlan County line (2); *Carter Co.,* Carter Caves (4); *Floyd Co.,* Wayland (2), Lackey Pond near Estill (2); *Harlan Co.,* Big Black Mountain (3); *Henderson Co.,* (1); *Larue Co.,* 6 mi. E White City (1).

MAINE—*Cumberland Co.,* Cape Elizabeth (1); *Kennebec Co.,* Vassalborough (1); *Oxford Co.,* Bethel (8), Norway (5); *Penobscot Co.,* Orono (38), Wattawankeag Township (9), Old Town (1); *Sagadahoc Co.,* Brunswick (1); *Somerset Co.,* .5 mi. S The Forks (4), Parland Pond Township (5), Tarrantine (10); *York Co.,* Limington (1), Saginaw (1), Trenton (3), Richardson Lake (1).

MARYLAND—*Cecil Co.,* Bacon Hill (6); *Garrett Co.,* Jennings (10).

MASSACHUSETTS—*Berkshire Co.,* Williamstown (4); *Essex Co.,* Lynn (1), Salem (5), West Manchester (1); *Hampden Co.,* Springfield (5); *Hampshire Co.,* Northampton (4), Worthington (8); *Middlesex Co.,* Concord (2), East Lexington (1); *Norfolk Co.,* Wellesley (1); *Suffolk Co.,* Arlington (15), Cambridge (18), Newton (1), Mattapan (2), Warwick (1).

MICHIGAN—*Allegan Co.,* 2 mi. SW Glenn (1), Wayland (13), others (2); *Alpena Co.,* (8); *Berrien Co.,* 3 mi. N Three Oaks (1), Harbert (14),

Warrens Woods (7); *Calhoun Co.,* (1); *Cass Co.,* Diamond Lake (2); *Charlevoix Co.,* Pine Lake (1), Boyne Lake (3), Thumb Lake (1), Beaver Isle (1), others (1); *Cheboygan Co.,* Douglas Lake (13), Monroe Lake (1), others (3); *Emmet Co.,* Round Lake (2); *Kalamazoo Co.,* 10 mi. SW Kalamazoo (1); *Keweenaw Co.,* Forbes Lake (1), Island in Tobin Harbor (14), Isle Royale, Chickenbone Lake (2), Keweenaw Point, 2 mi. S Copper Harbor (21); *Montmorency Co.,* (4); *Otsego Co.,* Pigeon River Trout Research Area (7), others (3); *Presque Isle Co.,* (1); *Van Buren Co.,* South Haven (10), others (1); *Washtenaw Co.,* Superior Township, north of Dixboro (29), Ann Arbor Township, Section 24 (2), Section 30 (11), Freedom Township, Section 9 (3), Lodi Township, Section 6 (16), Seis Township, Section 28 (3).

MINNESOTA—*Anoka Co.,* Mississippi River, Fridley (1), Coon Creek (3); *Becker Co.,* Tamarac Lake (1); *Beltrami Co.,* Moose Lake (2), others (2); *Carlton Co.,* Colquet State Forest (5), Moose Lake Region (1); *Cass Co.,* Cass Lake, Pike Bay (2), Ten Mile Lake (10), Woman Lake (1); *Clearwater Co.,* Itasca Park (73); *Cook Co.,* Grand Portage (2); *Crow Wing Co.,* Gull Lake Biological Station (5); *Hennepin Co.,* Minneapolis (1), Nine Mile Creek (1); *Itasca Co.,* (6); *Kittson Co.,* Lancaster (8), St. Vincent (1), Northcote (1), 6 miles northwest Lake Bronson (3); *Koochiching Co.,* Ericsburg (2); *Lake Co.,* Lake Saganaga (7), Knife River (1); *Marshall Co.,* Thief Lake (5), 3 mi. E Warren (3), 5 mi. S Strandquist (5), Moose River (1); *Mille Lacs Co.,* (1); *Morrison Co.,* Motley (1); *Pine Co.,* southeastern part (13); *Polk Co.,* Fertile (6); *Rice Co.,* Strand Woods (3); *Roseau Co.,* Warread, Camp Grounds (3); *Saint Louis Co.,* Eveleth (4), Lake Esquagana (2), Duluth (1), Camp Warren (3), West Branch Lester River (1); *Wadena Co.,* Redeye River near Sebeka (3); *Washington Co.,* Stillwater (2), others (1); Birchdale (1); Lake Superior (1).

MISSOURI—*Saint Louis Co.,* (1); *Stone Co.,* near Marble Cave (4).

MONTANA—*Yellowstone Co.,* Billings (2)? (poor preservation).

NEW HAMPSHIRE—*Belknep Co.,* West Alton (1); *Cheshire Co.,* 4 mi. SW Fitzwilliam Depot (1), 2 mi. NE Northfield, Mass. (1); *Coos Co.,* near Pittsburg (1), 9 mi. NW Berlin (1), Mount Washington, Oakes Golf (1), Milan (4); *Grafton Co.,* 2 mi. NE Thornton (1); *Hillsboro Co.,* 3.5 mi. NE Hudson (1), Contoocook River, NE Antrim (1), 3 mi. NE Amherst (1); *Merrimack Co.,* New Hampten (1), Hackett (1), 3 mi. NE Boscawen (3), Penacoo Lake near Concord (6).

NEW JERSEY—*Bergen Co.,* Hackensack (2); *Burlington Co.,* Indian Mills (2), Medford (3); *Cape May Co.,* Cedar Swamp Creek (1); *Morris Co.,* Budd's Lake (1).

NEW YORK—*Albany Co.,* Rensselaer (2); *Chemung Co.,* (7); *Greene Co.,* Haines Falls (1); *New York Co.,* Bronx (2); *Schoharie Co.,* Howe's Cave (2); *Schuyler Co.,* Alpine (4), Cayuta Lake (5), others (3); *Tioga Co.,* Waverly (20); *Tompkins Co.,* Ringwood (5).

NORTH CAROLINA—*Avery Co.,* Grandfather Mountain (1), near Banners Elk (2), Linville (1); *Buncombe Co.,* Swannanoa (2); *Cherokee Co.,* 2 mi. ESE Andrews (15), 2 mi. SE Murphy (9); *Clay Co.,* 3 mi. SE Brasstown (1); *Madison Co.,* Marshall (1); *Rutherford Co.,* Chimney Rock (1); Beaver Creek (1).

NORTH DAKOTA—*Stutsman Co.,* 1 mi. N Jamestown (2); *Rolette Co.,* Bluebill Lake, Turtle Mountains (40).

OHIO—*Adams Co.*, (1); *Ashland Co.*, Mifflin Township (1); *Ashtabula Co.*, Pymatuning Lake, near Richmond Center (1), Monroe Township (20); *Brown Co.*, (1); *Clermont Co.*, (9); *Delaware Co.*, Radnor (1); *Fairfield Co.*, Violet Township (28), Berne Township (3); *Hooking Co.*, Salt Creek (3), Conkle's Hollow (11), Old Man's Cave (2), Rock House (2), 4 mi. ENE Logan (3), Ash Cave (1), Benton Township (9), Salt Creek Township (3), South Perry (6), Clear Creek (16); *Lucas Co.*, Toledo (14), Richfield Township (17); *Mahoning Co.*, Boardman (2); *Stark Co.*, Massilon (10); *Summit Co.*, Richfield (1); *Warren Co.*, Fort Ancient State Park (3); *Washington Co.*, Fairfield Township (2); *Wayne Co.*, (1); *Williams Co.*, Blakeslee (2); Northwest Township (10).

PENNSYLVANIA—*Allegheny Co.*, Squaw Run, near Pittsburgh (9), Squaw Run, near Aspinwall (10); *Blair Co.*, (2); *Carbon Co.*, Hickory Run (9); *Chester Co.*, (2); *Crawford Co.*, Pymatuning Swamp (1); *Indiana Co.*, (5); *Juniata Co.*, (1); *Lehigh Co.*, (1); *Lycoming Co.*, Ellenton (2); *Mifflin Co.*, (2); *Monroe Co.*, Porono Lakes (52); *Warren Co.*, Starbrick (3), Akley (1).

SOUTH CAROLINA—*Oconee Co.*, Salem (1), 16 mi. N Seneca (1); *Pickens Co.*, 14 mi. NE Pickens (1).

TENNESSEE—*Sevier Co.*, Gatlinburg (1).

VERMONT—Bridgeport (1); Killington Park (1).

VIRGINIA—*Bath Co.*, Hot Springs, Cave Run (1); *Giles Co.*, Salt Pond Mountain, Mountain Lake Biological Station (1); *Henry Co.*, Spencer (1); *Fairfax Co.*, Great Falls (3).

WASHINGTON—Puget Sound (7) (?).

WEST VIRGINIA—*Grant Co.*, 3 mi. W Mount Storm, near Stoney River (7); *Greenbrier Co.*, Caldwell (1); *Hampshire Co.*, Romney (1); *Hardy Co.*, 4 mi. SE Moorefield (1); *Kanawha Co.*, Belle near Du Pont (1), Kanawha City (1); *Monongalia Co.*, Cooper's Rock (1); *Nicholas Co.*, Camp Woodbine (1), Snake Den Mountain (2); *Pendleton Co.*, 2 mi. N Franklin (1), Spruce Knob (3); *Pocahontas Co.*, Cranberry Glades (5), Cranberry Mountain (1), Watega State Park, Seebert Arboretum (1), Camp Thornwood (2), Traveller's Repose (1), Spice Troop Mountain State Park (2), Marlinton (1); *Putnam Co.*, Winfield (2); *Randolph Co.*, Elkins (3), Barton Knob (7), Kerens (3), Shaver's Mountain near Elkins (1), Laurel Mountain (1), 4 mi. S Elkins (1), White Top Mountain (2), Bickle Knob (3), 1 mi. E Norton (2); *Tucker Co.*, Moore (2).

WISCONSIN—*Ashland Co.*, (1); *Burnett Co.*, 3 mi. S Webster (1); *Chippewa Co.*, Cornell (2); *Lincoln Co.*, 3 mi. E Doering (3), Merrill (2); Copper River (1); *Marathon Co.*, Big Rib River, 3 mi. W Marathon City (1); *Rush Co.*, 5 mi. N Ladysmith (1), Hawkins (1); *Sawyer Co.*, Windfall Lake, 1 mi. E Exeland (1); *Taylor Co.*, 7 mi. N Medford (1); *Vilas Co.*, Trout Lake, S of Boulder Junction (24); *Waukesha Co.*, Wauwatosa (36); *Wood Co.*, Sharry (2).

WYOMING—*Albany Co.*, 6 mi. WNW Centennial (2), Lake Irene (5), Trail's Divide Pond (5).

ALASKA—Bettles (35); College (1); along railroad halfway between College and Fairbanks (55); near Fairbanks (20); Fort Yukon (2); 10 mi. SE Kenai (1); Kobuk, Kobuk River (54); Matanuska Valley, 4 mi. N Palmer (7); Sergief Island, N of Stikine River (5); Situk River (1); Yakutat (6).

CANADA

ALBERTA—Athabaska River (5), Athabaska River Delta (2), Beaver Hill Lake (1), Bragg Creek (W of Calgary) (2), 7 mi. S Camrose (8), Cold Lake (1), Coronation (2), Cottage Lake (13), Delburne (2), Devil's Lake (1), Edmonton (13), Elnora (1), Fort Chilewayan (1), Gorge Creek (W of Turner Valley) (4), Grovedale (6), Hardisty (1), Hines Creek (56 deg. N.) (1), Indian River Cabins (60 deg. N.) (5), Johnson Lake, Banff Park (5), Lac La Biche (1), Lousana (2), Malnook (1), Muskeget (2), Muskegs, Fawcett (5), Nordegg (6), Porcupine Hills (W of Lethbridge) (3), Pyramid Lake, Jasper Park (5), Rock Lake (7), 25 mi. W entrance to Rock Lake (1), Rocky Mountain Park (1), St. Paul (1), Square Lake (9), Stettler (1), Trapper's Lake (nr. Elk Island Park) (6), Villeneauve (3), Wabamun Lake (8), Winterburn (2).

BRITISH COLUMBIA—Atlin, Como Lake (1), 3 mi. E Atlin (5), Caribou (1), Charlie Lake (4), 9 mi. N Clinton (1), Driftwood River near Tetana Lake (1), Driftwood River near Bunshaw Trail Pond (2), Indian Point Lake (1), Issac Lake, Barkersville (1), Kispiox Valley, Hazelton (2), 23 mi. N Hazelton (3), 49 mi. W Hazelton (5), Susan Lake, Tupper Creek (1), Telegraph Creek, Hay Meadow Lake (9), Tetana Lake (6), Tupper Creek and Lake (8).

LABRADOR—Hamilton River, Muskrat Falls (1), Hamilton Inlet, 25 mi. SW Northwest River (7), Mud Lake, near mouth Hamilton River (4), Northwest River (village) (6).

MANITOBA—Brandon (1), Carberry (1), Cedar Lake (2), Churchill (2), Delta (2), Gypsonville (14), Horseshoe Lake (6), Ilford (26), Jackhead Reservation (2), Lake St. Martin Ind. Res. (6), Lake Saskatchewan (1), Lake Winnipeg (4), Red River (2), The Pas (16), Wabowden (11).

NEW BRUNSWICK—Long's Creek (1), McNamee (1), Fredericton (1), Shippigan (1).

NORTHWEST TERRITORIES—Great Slave Lake, Moraine Bay (5), Great Slave Lake (18), Hay River, Old Settlement (4), Husky River below Peel River (1), MacKenzie River Delta (1), Norman Wells, Bear Island (3).

NOVA SCOTIA—*Annapolis Co.*, (1), Breton Island off Cape Breton (6); *Digby Co.*, Cedar Lake (1), Goldmine Brook, Moser River (1); *Halifax Co.*, Oakfield (1), Liverpool (1), Orangedale (1); *Yarmouth Co.*, Quinan (1).

ONTARIO—*Algoma District*, Gros Cap (1), Laird (36), Lake George (4), Little Rapids (1), Maclennan (33), Mississagi River (1), Pine Island (1), St. Joseph Channel (4), St. Joseph Island (5), Whitefish Bay, Isle Parisienne (3); *Bruce Co.*, Kincardine (1), Lucknow (4); *Bryant Co.*, New Durham (2); *Cochrane District*, Fort Albany (16), Fraserdale (36), Genier (1), Halfway Point (11), Hannah Bay (1), Lake Abitibi (26), Lake Long, 10 mi. S Cochrane (2), Monsonee (52), 8 mi. N Montieth (10), Moose Factory, James Bay (6), Nagami River (2), Nettichi Point (13), Onakawana (10), Palmquist River (4), Pitopiko River (1), Shelak River, E of Hearst (2), Ship Sands (3), Smoky Falls (8), Tidal Creek (1), Timmons (7); *Dufferin Co.*, Grand Valley (2); *Durham Co.*, Clarke Twp. (1), Courtice (1); *Frontenac Co.*, Arden (16), Camp Oconto (2), Eagle Lake (2), Mount Grove (14), Parkham (1), others (6); *Glengarry Co.*, Spring Creek, Brodie (4), Bainsville (2); *Gray Co.*, Cape Rich (1); *Grenville Co.*, Fairfield (1); *Haliburton*

Co., Miner's Bay (7), Mountain Lake (1); *Halton Co.,* Oakville (1), Sixteen Mile Creek (2); *Huron Co.,* Landesborough (1); *Kenora District, Malachi* (2); *Kent Co.,* Rondeau Park (17); *Lennox Co.,* Abinger Twp. (2), Buckshot Lake (1); *Leids Co.,* Black Rapids (4), Gananoque (2), Warburton (2), Willys' Branch, South Lake (5); *Lincoln Co.,* St. Catherine's (1); *Manitoulin District,* Cockburn Island (1), Little Current (1), Manitoulin Island (3), Sonding Cove, Manitoulin (1); *Middlesex Co.,* London (3); *Muskoka District,* Bala (2), Mactier (2), Muskoka (4), Muskoka Lake, Mortimer Point (1); *Nipissing District,* Algonquin Park (20), North Bay (5), Tamagami (8); *Norfolk Co.,* St. Williams (8), Turkey Point (4); *Northumberland Co.,* Brighton (1); *Ontario Co.,* Greenwood (1), Oshawa (2), Uxbridge (1); *Parry Sound District,* Lake Nipissing (8), Parry Sound (5); *Patricia District,* Borthwick Lake (26), Cape Henrietta Maria (10), Favourable Lake (11), Fort Severn (40), Lake Attawapiskat (12); *Peel Co.,* 10 mi. NE Brampton (1), Caledon (4); *Peterboro Co.,* Oak Lake (3), Silver Lake (1); *Prince Edward Co.,* Hallowell (1), Picton (9), Pleasant Bay (1), Wellington (10); *Rainy River District,* Agnes Lake, Quetico Provincial Park (4), others (16); *Renfrew Co.,* Petawawa Reserve (1); *Simcoe Co.,* Egbert (1), Tossorontia Twp. (1), Utopia (1); *Stormont Co.,* Doherty Creek (1); *Sunbury District,* Montreal River (1), Spanish River (2); *Thunder Bay District,* Chippewa Park, Fort William (5), Jarvis Lake, near Umphey (3), Lake Nipigon (70), Long Lac (3), McIntosh Lake (1), 20 mi. E Port Arthur (2); *Waterloo Co.,* Galt (1), Kitchener (1); *Wentworth Co.,* Hamilton (1); *York Co.,* King Twp. (31), Klineburg (1), Lambton Mills (1), Malvern (1), Marie Lake (1), Mount Dennis (1), Musselman's Lake (3), Pottageville (6), Summerville (1), Toronto (16), Vandorf (2), Wilcox Lake (8), Woodbridge (1).

PRINCE EDWARD ISLAND—Charlottetown (1), Sauris (1).

QUEBEC—*Bonadventure Co.,* (1), Great Whale River (mouth) (1), Lac aux Sables (1), Mingan Island (3), Point Comfort (2), Richmond Gulf (5), others (1).

SASKATCHEWAN—Indian Head (1), Lac la Rouge (3), Lake Athabaska (9), Kamsack (2), Prince Albert Nat. Park (1), Waskesiu, Narrows Bay (6), Waskesiu Lake (16), Yorkton (1).

YUKON TERRITORY—Duane Lake (5), Forty Mile Creek (4), Taklin River at crossing of Army Road (3).

REFERENCES

ALLEE, W. C. ET AL. 1949—Principles of animal ecology. Phila., W. B. Saunders Co.

BAIRD, S. F. 1854—Descriptions of new genera and species of North American frogs. Proc. Acad. Nat. Sci. Phila. **7**:59-62.

BARGHOORN, E. S. 1953—Evidence of climatic change in the geological record of plant life. *In,* "Climatic change: evidence, causes, and effects." Cambridge, Harvard Univ. Press. 235-248.

BLEAKNEY, S. 1952—The amphibians and reptiles of Nova Scotia. Canadian Field-Naturalist **66**:125-129.

BORGMEIER, T. 1957—Basic questions of systematics. Syst. Zool. **6**:53-69.

BOULENGER, G. A. 1920—A monograph of the American frogs of the genus *Rana.* Proc. Amer. Acad. Arts, Sci. **55**:413-480.

BRECKENRIDGE, W. J. 1944—Reptiles and amphibians of Minnesota. Minneapolis, Univ. of Minn. Press.

BREUKELMAN, J. AND H. H. SMITH 1946—Selected records of reptiles and amphibians from Kansas. Univ. Kansas Publ. Mus. Nat. Hist. **1**:101-112.

BROWN, W. L., JR. AND E. O. WILSON 1954—The case against the trinomen. Syst. Zool. **3**:174-176.

CONANT, R., E. S. THOMAS, AND R. L. RAUSCH 1945—The plains garter snake, *Thamnophis radix,* in Ohio. Copeia **1945**:61-68.

COPE, E. D. 1875—Check list of North American Batrachia and Reptilia. Bull. U. S. Nat. Mus. **1**:1-104.

———1886—Synonymic list of the North American species of *Bufo* and *Rana,* with descriptions of some Batrachia, from specimens in the National Museum. Proc. Amer. Phil. Soc. **23**:514-526.

———1889—The Batrachia of North America. U.S.Nat.Mus.Bull. **34**:1-525.

COTT, H. B. 1940—Adaptive coloration in animals. London, Methuen & Co., Ltd.

COWAN, I. M. 1939—The vertebrate fauna of the Peace River District of British Columbia. Occ. Pap. Brit. Prov. Mus. **1**:1-102.

DARLINGTON, P. J., JR. 1948—The geographical distribution of cold-blooded vertebrates. Quart. Review Biol. **23**:1-26, 105-123.

———1957—Zoogeography: The geographical distribution of animals. New York, John Wiley & Sons, Inc.

DICE, L. R. 1943—The biotic provinces of North America. Ann Arbor, Univ. of Mich. Press.

———1952—Quantitative and experimental methods in systematic zoology. Syst. Zool. **1**:97-104.

DILLON, L. S. 1956—Wisconsin climate and life zones in North America. Science **123**:167-176.

DOWDESWELL, W. H., R. A. FISHER AND E. B. FORD 1949—The quantitative study of populations in the Lepidoptera. Heredity **3**:67-84.

——— AND E. B. FORD 1952—The distribution of spot-numbers as an index of geographical variation in the butterfly *Maniola jurtina* L. (Lepidoptera: Satyridae). Heredity **6**:99-109.

FLINT, R. F. 1947—Glacial geology and the Pleistocene Epoch. New York, John Wiley & Sons.

FORD, E. B. 1954—Problems in the evolution of geographical races. *In* "Evolution as a Process." London, Geo. Allen and Unwin Ltd. 99-108.

GENTRY, G. 1955—An annotated check list of the amphibians and reptiles of Tennessee. J. Tenn. Acad. Sci. **30**:168-176.

GOIN, C. J. 1947—Studies on the life history of *Eleurtherodactylus ricordii planirostris* (Cope) in Florida. Univ. Fla. Studies, Biol. Sci. Ser. **4**:1-66.

GRANT, R. 1941—Salentia of the northern Pontiac County, Quebec. Copeia **1941**:151-153.

HARLAN, R. 1826—Descriptions of several new species of batracian reptiles with observations on the larvae of frogs. Amer. Jour. Sci. **10**:53-65.

HILDEBRAND, H. 1949—Notes on *Rana sylvatica* in the Labrador Peninsula. Copeia **1949**:168-172.

HOWE, R. H., JR. 1899—North American wood frogs. Proc. Boston Soc. Nat. Hist. **28**:369-374.

KENDREW, W. G. 1953—The climate of the continents. Oxford, Claredon Press.

LECONTE, J. 1825—Remarks on the American species of the genera *Hyla* and *Rana*. Ann. Lyc. Nat. Hist. New York **1**:278-282.

LIBBY, W. F. 1956—Radiocarbon dating. Amer. Scientist **44**:98-112.

LOBECK, A. K. 1948—Physiographic provinces of North America. Cambridge, The Geographical Press.

LOGIER, E. B. S. 1952—The frogs, toads and salamanders of eastern Canada. Toronto, Canada. Clarke, Irwin & Co.

MARTOF, B. S. 1956—Growth and development of the green frog, *Rana clamitans*, under natural conditions. Amer. Midl. Nat. **55**:101-117.

MASLIN, T. PAUL 1947—*Rana sylvatica cantabrigensis* Baird in Colorado. Copeia **1947**:158-162.

MAYR, E. 1954—Change of genetic environment and evolution. *In*, "Evolution as a process." London, Geo. Allen and Unwin Ltd. 157-180.

MECHAM, J. S. 1954—Geographic variation in the green frog, *Rana clamitans* Latreille. Texas Jour. of Sci. **6**:1-24.

MOORE, J. A. 1942—An embryological and genetical study of *Rana burnsi* Weed. Genetics **27**:406-416.

———1943—Corresponding genes in spotted frogs. Jour. Heredity **34**:3-7.

———1944—Geographic variation in *Rana pipiens* Schreber of eastern North America. Bull. Amer. Mus. Nat. Hist. **82**:345-370.

———1949—Patterns of evolution in the genus *Rana*. *In*, "Genetics, Paleontology, and Evolution." Princeton Univ. Press. 315-338.

———1949a—Geographic variation of adaptive characters in *Rana pipiens* Schreber. Evolution **3**:1-24.

OLIVER, J. A. 1955—North American amphibians and reptiles. Princeton, D. Van Nostrand Co.

PATCH, C. L. 1939—Northern records of the wood frog. Copeia **1939**:235.

PREBLE, E. A. 1902—A biological investigation of the Hudson Bay region. N. Amer. Fauna **22**:1-140.

———1908—A biological investigation of the Athabaska-Mackenzie region. N. Amer. Fauna **27**:501-502.

RENSCH, B. 1934—Kurze Anweisung für zoologisch-systematische Studien. Akademische Verlagsgesellschaft, Leipzig.

SCHMIDT, K. P. 1938—A geographic variation gradient in frogs. Zool. Ser. Field Mus. Nat. Hist. **20**:377-382.

———1953—A check list of North American amphibians and reptiles. 6th Ed. Am. Soc. Ich. and Herp.

——— AND W. L. NECKER 1935—Amphibians and reptiles of the Chicago region. Bull. Chicago Acad. Sci. **5**:57-77.

SCHOLANDER, P. F., W. FLAGG, R. J. HOCK, AND L. IRVING 1953—Studies on the physiology of frozen plants and animals in the Arctic. Jour. Cell. and Comp. Physiol. **42**:1-56.

SIMPSON, G. G. 1947—Evolution, interchange, and resemblances of the North American and Eurasian Cenozoic mammalian fauna. Evolution **1**:218-220.

SMITH, P. W. 1957—An analysis of post-Wisconsin biogeography of the Prairie Peninsula region based on ditributional phenomena among terrestrial vertebrate populations. Ecology **38**:205-218.

STEJNEGER, L. AND T. BARBOUR 1923—A check list of North American amphibians and reptiles. 2nd Ed. Cambridge, Harvard Univ. Press.

———1943—*Ibid.*, 5th Ed. Bull. Mus. Comp. Zool. **93**:xix+260 pp.

SUZUKI, H. K. 1951—Recent additions to the records of the distribution of the amphibians in Wisconsin. Trans. Wis. Acad. Sci. **40**:215-234.

THORSON, T. B. 1955—The relationship of water economy to terrestrialism in amphibians. Ecology **36**:100-116.

———1956—Adjustment of water loss in response to desiccation in amphibians. Copeia **1956**:230-237.

TRAPIDO, H. AND R. T. CLAUSEN 1938—Amphibians and reptiles of eastern Quebec. Copeia **1938**:117-125.

TURNER, L. M. 1886—Contributions to the natural history of Alaska, Part IV (Fishes). Arctic Series, Signal Service, Wash., No. 2, 87-113.

VOLPE, E. P. 1955—Taxo-genetic analysis of a mutant frog. Syst. Zool. **4**:74-82.

WALKER, C. F. 1946—The Amphibians of Ohio. Part I. The frogs and toads. Ohio State Arch. and Hist. Soc. **1**:109 pp.

WEIZ, S. AND A. S. PACKARD, JR. 1866—List of vertebrates observed at Okak, Labrador. Proc. Bost. Soc. Nat. Hist. **10**:264-277.

WILSON, E. O. AND W. L. BROWN, JR. 1953—The subspecies concept and its taxonomic application. Syst. Zool. **2**:97-111.

WILSON, L. W. 1945—Amphibians of Droop Mountain State Park. Proc. W. Va. Acad. Sci. (1944), W. Va. Univ. Bull. **45**:39-41.

WITSCHI, E. 1953—The cherokee frog, *Rana sylvatica cherokiana nom. nov.*, of the Appalachian Mountain region. Proc. Iowa Acad. Sci. **60**:764-769.

WRIGHT, A. H. AND A. A. WRIGHT 1933—Handbook of frogs and toads. 1st Ed. Ithaca, N. Y., Comstock Publ. Co.

——— AND ———1942—*Ibid.* 2nd Ed.

——— AND ———1949—*Ibid.* 3rd Ed.

WYNNE-EDWARDS, V. C. 1952—Freshwater vertebrates of the Arctic and Subarctic. Canada Fisheries Research Board Bull. **94**:1-28.

YEARBOOK OF AGRICULTURE 1941—Climate and man. U. S. Dept. of Agriculture, House document No. 27.

Some Effects of Starvation on the Larval Cuticle of Persectania ewingii (Wwd.) (Lepidoptera: Noctuidae)

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In years when the environmental conditions favour it, the larvae of *Persectania ewingii* (Wwd.) display typical army-worn behaviour. This is characterized by an irresistible urge to wander, which frequently causes swarms of larvae to leave areas containing ample food and to enter areas where none of their food plants is growing. During the ensuing period of starvation, the larvae draw upon their reserve storage which, in fifth-larval instars, is exhausted towards the end of their fourth foodless day. They are then in a weakened state, but are able to survive for a further 20 to 30 hours by making use of materials which become available through catabolic changes in their cuticles. If, at the end of this time, they do not obtain food, the larvae die from inanition.

This study deals with the proportions of water, and of selected constituents of the dry matter, in the cuticles of feeding larvae; and compares these with the proportions of the same components in the cuticles of (1) larvae from which food was withheld for 5 days, and (2) larvae which after being deprived of food for 5 days, were permitted to feed for 24 hours. Structural changes in the cuticle associated with starvation are also considered.

The swarming condition was artificially induced by rearing many larvae in a restricted space under controlled environmental conditions. Until selected for testing, a large excess of food was constantly available.

Preparation of Cuticles

All larvae used were killed with cyanide, and from each, the head and the posterior abdominal segment with its pair of larvapodia were removed. A longitudinal, mid-ventral cut along the full length of the body then enabled the greater part of its contents to be disposed of. All appendages were individually excised because it was impracticable to free these from their internal tissues. Final cleaning was done under a low-power binocular microscope, using small swabs of cotton wool on the ends of toothpicks. Batches of cuticles were prepared by both the "dry" and the 70 percent ethanol methods of Fraenkel and Rudall (1947), the former being used when water content of the cuticle was to be determined, the latter when changes in composition of its dry matter were being investigated.

While mechanical methods of cleaning are indispensable for work

of the kind contemplated, their inherent defects must be taken into account when quantitative results are aimed at. At best, they are crude, and this imposes definite limits on the degree of accuracy with which data obtained by their use can be interpreted. Recent work of the late E. L. Schmidt (1956) indicates that in many insects, a layer of material, his "sub-cuticle," separates the procuticle from the hypodermis. Such a layer occurs in the larvae of *Persectania*. In the final stages of cleaning, irrespective of the care exercised, varying proportions of both the "sub-cuticle" and the innermost part of the procuticle are removed, as can readily be demonstrated by embedding and sectioning cleaned cuticles, and examining the stained sections under the microscope. A difficulty peculiar to the "dry" method is that in the course of their preparation, the cuticles are inevitably exposed at different times, and for different lengths of time, to air whose temperature and relative humidity fluctuate. The cuticles are hygroscopic, and hence may absorb water from moist air; alternatively, they may lose water to a dry atmosphere. Time of exposure cannot be reduced below the minimum necessary for adequate cleaning, and the above-mentioned factors may produce a discrepancy in the water content of as much as 5 percent of the minimum ascertained value within a group (see Table I).

THE WATER CONTENT OF THE CUTICLE

To determine water content of the cuticle, three batches each of 30 larvae were selected from each of three groups: feeding larvae; larvae which had been starved for 5 days; and larvae which, after having been starved for 5 days, had been permitted to feed for 24 hours (hereafter referred to as groups A, B, and C, respectively.) The 9 batches of cuticles were separately weighed, and then dehydrated at 102°C. The values for individual batches and the means for the three batches of each group are shown in Table I.

Although variation between batches of a group may be as large as 5 percent of the minimum ascertained value, the differences are small compared with those which distinguish group B from the other two; and it is evident that the cuticles of starved larvae have a much higher water content than have those of larvae which are feeding. There is, however, no evidence which can be offered in explanation of this fact.

PROPORTIONS OF CONSTITUENTS OF THE DRY MATTER IN THE CUTICLE

The larvae used for this part of the work were selected from the same three groups as were used for determination of water content of the cuticle. The method of Fraenkel and Rudall (*op. cit.*) for separating the dry matter of the cuticle into three fractions (their "water-soluble protein, or arthropodin," "non-chitinous constituents," and "chitin," respectively), was adopted.

The considerable advances made in cuticular chemistry since 1947 indicate a higher degree of chemical complexity in the cuticle than has hitherto been recognized. As Richards (1958) points out, evidence is accumulating which tends to cast doubt on the presence of either protein or chitin as such in the cuticle. These substances may possibly be the degradation products of chemical treatment of the cuticle in the laboratory. Because some of the results obtained in this investigation are more comprehensible if this possibility is borne in mind, and because starvation considerably modifies the chemical composition of some of the cuticular components, the simple descriptive appellations —"water extract," "alkali extract," and "non-extractable fraction"— which raise no questions as to the chemical nature of the three fractions, have been substituted for the terms of Fraenkel and Rudall.

To determine the proportions of the three fractions, the cuticles were first dried to constant weight at 102°C.

The nine batches were separately extracted under reflux in two changes of boiling water, each for 12 hours. At the end of this time, the two extracts were united and kept. The batches, after washing in water, were dried to constant weight at 102°C, the loss in weight being that of the water extract. They were then separately extracted under reflux in two changes of boiling 5 percent aqueous potassium hydroxide solution, each for 12 hours, the extracts being retained as before. At the end of this time, the cuticles were soaked for 10-minute periods in each of the following: 70 percent ethanol, distilled water, distilled water acidified with two or three drops of concentrated hydrochloric acid, and two changes of distilled water. They were then dried to constant weight at 102°C. This weight was that of the non-extractable fraction; its difference from the previous weighing represented the weight of the alkali extract. The three fractions of each batch were later used for nitrogen determination.

Two points may be here referred to: the times of extraction, and the method of washing the non-extractable fraction. Preliminary trials showed that prolonging extraction times beyond 24 hours made no measurable differences in the weights obtained. The washing procedure following alkali treatment was necessitated by the adsorption by the non-extractable fraction of large quantities of potassium hydroxide from the extracting solution. Water alone would not remove this.

In Table I are shown the weights and proportions of the three cuticular fractions of each of the 9 batches of cuticles examined. Because of the shortcomings of the method of cleaning the cuticles, figures have been corrected to the nearest unit; allowance should be made for a maximum possible error of $\pm$ 1 percent.

Within any one group, variations between batches are negligible, being very small compared with inter-group differences. The proportions for groups A and C are practically identical, the ratio being 35 : 29 : 36. These values approximate to those obtained by Fraenkel and Rudall for some of the species they investigated. Thus, of

TABLE I.—Weights and proportions of major constituents of cuticles of A, feeding larvae; B, larvae starved 5 days; C, larvae starved 5 days; then fed for 1 day

Group	Batch	Dry matter in each batch (mg)	Dry matter in: Water extract (mg)	Dry matter in: Alkali extract (mg)	Dry matter in: Non-extractable fraction (mg)	Water content of "fresh" cuticle (%)
A	I	236	82 (35%)	69 (29%)	85 (36%)	60
	II	234	80 (34%)	68 (29%)	86 (37%)	62
	III	243	82 (34%)	73 (30%)	88 (36%)	59
Totals		713	244	210	259	—
Means		238	81 (34%)	70 (29%)	86 (36%)	60
B	I	219	63 (29%)	64 (29%)	92 (42%)	73
	II	214	63 (29%)	63 (30%)	88 (41%)	75
	III	217	65 (30%)	63 (29%)	89 (41%)	73
Totals		650	191	190	269	—
Means		217	64 (29%)	63 (29%)	90 (42%)	74
C	I	237	81 (34%)	70 (30%)	86 (36%)	61
	II	241	84 (35%)	70 (29%)	86 (36%)	64
	III	238	83 (35%)	69 (29%)	87 (36%)	62
Totals		716	248	209	259	—
Means		239	83 (29%)	70 (35%)	86 (36%)	62

Dixippus, they found that a total of 63.5 percent of the dry matter of the cuticle was extractable and 36.5 percent non-extractable. Their corresponding figures for *Locusta* were 63.1 percent and 36.9 percent. Unfortunately they did not state the proportions of the two extractable fractions separately.

The ratio of the components of the cuticles of starved larvae — 29 : 29 : 42 — is markedly different from that of the other two groups. Its proportion of water extract is 6 percent below, that of its non-extractable fraction 6 percent above, that of feeding forms. Consideration of the proportions alone, however, merely shows that starvation has modified these; it affords no information as to how this modification has been achieved. The latter can be appreciated only after changes in weight have been studied.

The mean gross weight of the dry matter of a batch of cuticles of starved larvae is 21 mg less than that of feeding larvae (group A), demonstrating an actual loss of this quantity of material from the cuticle. But the combined total of the extractable fractions shows that these have lost 24 mg — 17 mg from the first, and 7 mg from the second. The difference between the 21 mg lost from the cuticle as a whole, and the 24 mg withdrawn from the two extractable fractions is accounted for by the 3 or 4 mg of material which the non-extractable fraction has gained.

When feeding re-commences, the processes which bring about the changed proportions in the cuticles of starved larvae, now operate in reverse. At the end of about 24 hours after resumption of feeding, the proportions of the three cuticular fractions are restored to what they normally are.

While the above facts demonstrate that, in emergency, the material in the cuticle can be drawn upon, to be later replaced if or when circumstances permit, much more is involved than a mere "banking transaction." Evidence presented in the next section demonstrates that, during starvation and during recovery, far-reaching changes in composition of all three fractions occur.

Comparison of the Nitrogen Content of the Three Cuticular Fractions of Feeding and Starved Larvae

The proportions of nitrogen in the three cuticular fractions (Table II) were obtained by the use of the micro-Kjeldahl method, the ammonia being determined colorimetrically with Nessler's reagent.

Accepting the value of 16 percent as representing the approximate nitrogen content of a simple cuticular protein (Lafon, 1943), then the water extract of feeding larvae consists very largely, and that of starved larvae almost wholly, of such protein. This may be the "arthropodin" of Fraenkel and Rudall (*op. cit.*).

The much lower proportions of nitrogen in both alkali extracts suggest that these are composed either of a mixture of protein and non-nitrogenous material, or of a conjugated protein, such as a glycoprotein of low nitrogen content. That different materials, or at

TABLE II.—Proportions and weights of nitrogen in the three cuticular fractions of feeding and starved larvae (all values are the means of three determinations)

Fraction	Nitrogen in dry matter				Gain or loss in weight of N (starved larvae) (mg)
	Feeding larvae (A)		Starved larvae (B)		
	(%)	Calculated weight (mg)	(%)	Calculated weight (mg)	
Water extract	13.08	11	15.81	10	—1
Alkali extract	7.62	5	10.06	6	+1
non-extractable	6.06	5	8.71	8	+3

least, different proportions of the same materials, are present in the respective alkali extracts is evident from the much higher nitrogen content of this fraction in starving larvae.

The greatest difference in nitrogen content appears between the two non-extractable fractions. The proportion of nitrogen in that of feeding larvae is sufficiently near the theoretical 6.9 percent, (ash being ignored), to indicate that it consists almost wholly of chitin. The corresponding fraction of starved larvae must contain matter of high nitrogen content additional to chitin for its proportion of nitrogen to be as high as 8.71 percent.

When percentages of nitrogen are transformed to weights, it is seen that equal weights of nitrogen (16 mg) are present in the extractable part of the cuticles of both feeding and starved larvae; but the non-extractable fraction of starved larvae contains 3 mg more of nitrogen than does this fraction of feeding larvae. While it may be fortuitous, the fact that this increase is about equal to the total increase in weight of the fraction (see Table I), suggests that during starvation, additional nitrogen is stored in the non-extractable fraction. Since the total weights of nitrogen in the extractable part of the cuticles of both feeding and starved larvae are the same, the source of the additional nitrogen stored would appear to be extracuticular.

Expression of the percentages of nitrogen in the fractions in terms of "protein" and "chitin," respectively (Table III), shows that during

TABLE III.—"Protein" and "Chitin" in the cuticles of feeding and starved larvae

Larval condition	Water extract			Alkali extract			Non-extractable fraction		
	"Protein" (mg)	Non-nitrogenous (mg)	Total (mg)	"Protein" (mg)	Non-nitrogenous (mg)	Total (mg)	"Chitin" (mg)	Non-nitrogenous (mg)	Total
Feeding	66	15	81	33	37	70	76	10	86
Starved	63	1	64	40	23	63	—*	?	90

* Sufficient nitrogen to account for 114 mg of "chitin"

starvation the cuticle tends firmly to retain nitrogen. Thus the "protein" of the water extract of starving larvae is only slightly less, that of the alkali extract considerably more, than the corresponding values for feeding larvae. The principal drain is from the non-nitrogenous moieties of the extractable fractions. Of these, the water extract of starved larvae has lost practically all, while the alkali extract has lost about 40 percent. Of the total extractable non-nitrogenous constituents originally present, starvation has halved the quantity.

The "chitin" of feeding larvae constitutes about 90 percent of the non-extractable fraction; but there is sufficient nitrogen in this fraction of starved larvae to provide 114 mg of chitin, though the whole fraction weighs only 90 mg. In this case, the fraction can contain little non-nitrogenous matter, but has acquired extra material of high nitrogen content.

The figures discussed in this section clarify those given on page 394. The 24 mg lost from the extractable fraction consist largely, if not entirely, of non-nitrogenous matter; the 3 mg gained by the non-extractable fraction represents nitrogenous matter of extra-cuticular origin.

STRUCTURAL CHANGES IN THE CUTICLE ASSOCIATED WITH STARVATION

That starvation induces both chemical and structural changes in the cuticle can be demonstrated by sectioning larvae from each of the three groups, and examining the stained sections microscopically. Most of the cuticle consists of endocuticle which, in feeding larvae, stains uniformly with the dyes commonly used for this purpose (e.g. aniline blue or methyl green). The "endocuticles" of starved larvae fail so to respond; an outer zone stains normally, but the intensity of colour rapidly diminishes inwards, and large portions adjacent to the hypodermis either fail to stain, or even exhibit reversal of staining. When the latter happens, the areas take up the red of either the azocarmine G or the acid fuchsin. Now the latter effect is characteristic of that part of the procuticle which, by becoming impregnated with various materials, becomes the normal mesocuticle. It is possible, though there is no supporting evidence, that the added nitrogenous compounds by which the nitrogen content of the non-extractable fraction is increased during starvation, may resemble the natural impregnating materials, and hence be capable of producing similar changes, thereby giving rise to the pseudo-mesocuticular zones.

Within 30 hours of the re-commencement of feeding, the endocuticle resumes its normal staining reactions, except for a superficial layer of its innermost part which has been permanently modified. Using phase-contrast microscopy, this zone appears as a thin, dark line in unstained sections; in sections stained with methyl green, it is coloured deep blue-green in contrast to the much paler green of the remainder of the endocuticle.

When, after feeding has been resumed, the hypodermis again begins to secrete endocuticle, the altered zone demarcates the pre-starvation from the post-starvation parts. The union of the two is always weak, the newer-deposited material failing to knit firmly with the old. During sectioning, the two parts sometimes come asunder, the modified zone always remaining attached to the earlier-secreted endocuticle. Very occasionally, no union at all occurs, and the larva, in consequence, has a cleft endocuticle. When this happens, the inner endocuticle develops very irregularly, exhibiting sudden and great changes in thickness from place to place, and tending to be distorted. The width of the space between the two parts is not uniform. In some places, the adjacent surfaces may be contiguous; in others, a gap of as much as 20 μ may separate them. Larvae in this condition are capable of limited growth only; they may live for as long as 5 days, but the changes in preparation for moulting never begin, and they invariably fail to complete the stadium.

DISCUSSION

Some 20 years ago, Le Goffe (1939) reported that when he reared the fresh-water crustacean, *Lepidurus apus* Leach on a diet free from plant material, a progressive thinning of its cuticle was observable, from which he assumed that cellulose was an essential precursor of chitin. The lack of any quantitative data in his paper is much to be regretted for, as Whistler and Smart (1953) comment: "A corollary is that a part of the chitin may be consumed under certain conditions as a food reserve."

While this has never been demonstrated in insects, the present work establishes the fact that, at least in the larvae of *Persectania,* certain constituents of the cuticle can be so utilized, but only to a limited extent, and then in unusual circumstances. The non-nitrogenous moieties of its extractable fraction are those drawn upon, though the data in Table III do not exclude the possibility that a small amount of such material may come from the non-extractable fraction. Far from there being any evidence that "chitin" is consumed during starvation, the data point to its possible augmentation under these conditions. At least, nitrogen in a non-extractable form is added to it.

During starvation, two opposing processes are operating simultaneously in the cuticle. One, by removing non-nitrogenous matter from the cuticle tends to cause it to lose weight; the other, by bringing into the cuticle nitrogenous matter of extra-cuticular origin, and there storing it in a non-extractable form, exercises the opposite effect. Since the weight of material leaving, much exceeds that entering, the cuticle as a whole loses weight though the weight of its non-extractable fraction increases. Should feeding and development re-commence, the two processes reverse their mode of operation, and rapidly resynthesize the normal cuticular fractions. It is in connection with

this, that the additional water stored in the cuticle during starvation, may play an essential part.

This investigation has shown that there is a strong tendency for the ratio — percent of water extract : percent of alkali extract : percent of non-extractable fraction — to be maintained in the cuticle at the approximately-constant level of 35 : 29 : 36. Should this ratio be disturbed, forces directed towards its re-establishment assume control at the earliest possible moment. The importance to the larval economy of maintaining the cuticle intact is shown by the tenacity with which its components are held. Only after the general storage system has been exhausted does withdrawal of its dry matter begin, and its restoration has priority over all other storage. Within 20 to 30 hours of resumption of feeding, the three fractions revert to their original composition, though, during this time, no measurable quantity of material is returned to the general storage (Lower, unpublished data). Any relatively large change in the ratio is thus indicative of an impaired nutrition.

While the constancy of the ratio in normal feeding larvae argues in favour of secretion of the cuticle as a single complex compound, it does not dispose of the possibility of the individual secretion of its components. The crudity of the methods available for cleaning the cuticles limits the distinguishing of changes in the ratio to those which are relatively large, and makes recognition of small, but perhaps highly significant, changes impossible.

Consideration of the changes as a whole, makes it evident that withdrawal of dry matter from the cuticle is an abnormal phenomenon. When it occurs in nature, it is generally a prelude to death from starvation. The cuticle is not adapted to function as a normal, reserve, food-storage organ, and its enforced usage for this purpose is always to the detriment of the development on the rare occasions when the latter re-commences.

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REFERENCES

FRAENKEL, G., AND K. M. RUDALL 1947—The structure of insect cuticles. Proc. R. Soc. London, Series B **134**:111-143.

LAFON, M. 1943—Recherches biochimiques et physiologiques sur le squelette tégumentaire des arthropodes. Ann. Sci. nat. Zool. (Series 11) **5**:113-146.

LE GOFFE, M. 1939—Observations et expériences sur la biologie du *Lepidurus apus* Leach. Crustace phyllopode notostracé: Éthologie, croissance, régénération. Bull. Soc. Sci. Bretagne **16**:35-50.

RICHARDS, A. G. 1958—The cuticle of arthropods. Ergebn. Biol. **20**:1-26.

SCHMIDT, E. L. 1956—Observations on the subcuticular layer in the insect integument. J. Morph. **99**:211-226.

WHISTLER, R. L., AND C. L. SMART 1953—Polysaccharide Chemistry. Academic Press Inc., New York. Chapter XXVIII, 396.

A Review of the Status of Orconectes inermis Cope and a Suggested Nomenclatorial Change

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The blind crayfishes of the caves under the Cumberland Plateau have excited the curiosity of visitors and scientists since 1806. Written accounts are numerous and more than a century of conflicting literature has been produced. Hobbs brought this volume of material together when he revised the genus *Cambarus* in 1942.

Tellkampf (1844) described the blind crayfish from Mammoth Cave, Kentucky, under the name, *Astacus pellucidus*. Erichson (1846) placed it in his new genus *Cambarus* where it remained until Creaser (1933) raised Fowler's subgenus *Faxonius* to generic rank restricting the genus *Cambarus*. Hobbs found this status existing when he began working on the crayfishes in the late thirties. With the description of *Cambarus pellucidus australis* Rhoades (1941) from Alabama caves, it became evident that the hooks on the fourth walking legs represent a significant character for generic determination. In light of this new evidence, Hobbs (1942) redefined the genus. In naming the group, he pointed out that the genus *Faxonius* of Fowler (1912) was invalid by rule of priority. He further emphasized that one member of the genus had already been designated by the name *Orconectes* by Cope (1872). Thus, upon the erection and description of a separate genus, Cope's *Orconectes* must be applied. This generic change has met with popular approval and during the last fourteen years crayfish taxonomy has moved forward with new species described in most of the five new genera.

Cope, though an eminent zoologist, was not a student of crustacea. When he visited the Indiana caves with Professor E. T. Cox, the state geologist, public announcements were expected from this well-known scientist. The *Indianapolis Journal* of September 5, 1871 carried his "off-the-cuff" remarks regarding the mysterious denizens of the subterranean depths. The account specifically mentioned the blind crayfish, "*Astacus pellucidus*" given him by the state geologist. Cope's position as a carcinologist was hardly enhanced by his use of a generic name then nearly twenty-five years out of date! He did not even edit the error out of the account before it appeared in the *Annals and Magazine of Natural History* (1871: 368-370). In spite of his unfamiliarity with the field and apparently without consulting authorities on the group, he proceeded to name a new genus and a new species a few months later based upon a single second form male from Wyandotte Cave (Cope, 1872:419).

The publication had no sooner appeared than Dr. Hermann Hagen, who had revised and monographed the crayfishes the year before, published a stinging satire (Hagen, 1872) on the "hard-

driving evolutionist" and his "inhumane treatment of Mother Nature's kindred creatures." Dr. A. S. Packard, Jr., well-known zoologist and an authority on cave animals, also challenged Cope's new taxonomic creation. (Packard, 1872). The words of these two authorities brought an avalanche of adverse criticism that buried the name, *Orconectes inermis,* for seventy years.

The genus *Orconectes* established by Cope was poorly defined. His single character for erecting the genus was rudimental eyes with small, non-facetted cornea. No one has ever regarded this as having generic value in crayfishes. However, in the specific description which followed he mentioned that the Wyandotte Cave crayfish has hooks on the third and fourth walking legs. This character has been of value in separating the major groupings of the subfamily Cambarinae.

Pursuing the origin of the scientific name as a source of additional significant characteristics proved fruitless. The genus name, *Orconectes,* is derived from *Orcus,* the Roman god of the lower world, plus the Latin verb, *nectere,* meaning to bind or belong to. The species name, *inermis,* is from the Latin, *inerm,* meaning unarmed or toothless.

THE SPECIES PROBLEM

In light of Hobbs' revalidation of the genus *Orconectes,* we are now faced with the problem of the specific nomenclature of the smooth form of the blind crayfish from southern Indiana caves. The type specimen of *O. inermis* was collected from Wyandotte Cave, Crawford County, and was described as having a lack of spines and a short rostrum with sinuate, non-spinous margins. In 1893, Hay collected smooth crayfish with reduced spines from Mayfield Cave, Monroe County, which he admits as being allied to *inermis,* but described them under the name of *Cambarus pellucidus testii.* The seven characteristics compared below are common to Cope's description of *inermis* and Hay's description of *testii.*

O. inermis Cope (1872	*C. p. testii* Hay (1893)
1. Spines less developed.	1. Reduction of spines.
2. Marginal spines only angles or missing.	2. Lateral spines of rostrum wanting.
3. Basal lateral ridges marked and convergent; basal spines short.	3. Post-orbital ridges smooth and rounded at the ends.
4. Small patches of weak prickles on the sides of the carapace.	4. Lateral spines of carapace not more than a few low tubercles.
5. Frontal process considerably shorter; margins deeply sinuate.	5. Rostrum shorter than in Cope's *inermis* and running to a point in a gradual curve.
6. Third femora of the third and fourth walking legs with short hooks.	6. Hooks on the third walking legs short, blunt, and not curved; hooks on fourth walking legs variable.
7. Antennal lamellae much enlarged at the middle and contracted below; fringe of long hair.	7. Antennal scale shorter, broadest at the middle with longer spine.

These seven characters correlate very closely. Hay's more complete description points out several additional differences between the Indiana subspecies and the Kentucky species. After making the above comparisons, I conclude that *Cambarus pellucidus testii* Hay (1893) is synonymous with *Orconectes inermis* Cope (1872). Moreover, as will be shown later in the section on distribution and affinities, *O. inermis* intergrades freely with *O. pellucidus pellucidus* (Tellkampf) (1844) in the southern counties of Indiana. This leads me to suggest the name, *Orconectes pellucidus inermis,* for the smoother, less spinous subspecies of south central Indiana.

Orconectes pellucidus inermis Cope (1872) n. comb.

Type Locality.—Wyandotte Cave, Crawford County, Indiana.

Type Specimen.—One male, form II, presented to Dr. E. D. Cope by Prof. E. T. Cox, State Geologist of Indiana, prior to September 5, 1871. Though the type specimen has been reported by various authors as being in the collection of the Academy of Natural Sciences of Philadelphia, I have been informed that there is no indication that the specimen has ever been catalogued or deposited at the Academy.

Diagnostic Characteristics.—Rostrum short with terminal spine not extending beyond the apex of the antennal scale. Margins converging to an acuminate tip with lateral spines reduced to blunt angles or entirely missing. Post-orbital ridges low, smooth and blunt anteriorly. Lateral spines of the carapace represented by a few low granules. Cervical groove shallow and sinuate. Areola longer and slightly broader than that of specimens from the Mammoth Cave.

Flagellum of the antenna much elongated. Antennal scale broadest at the middle; apical spine long and acute. Fringe of hair longer than that of Kentucky specimens. Chelae somewhat heavier and lacking the tubercles and ridges of the typical *pellucidus.* Hooks on the third walking legs short and blunt and persistent. Hooks on the fourth walking legs variable and may exist in different condition on each leg, or even be entirely absent.

Neither Cope nor Hay saw any significant differences in the gonopods of the species and subspecies. The annulus ventralis of the female, however, differs considerably from the typical *pellucidus* of the Mammoth Cave. The annulus of *inermis* is nearly twice the length, breadth and height of the annulus of Kentucky specimens. It appears that the central prominence has become much elevated, even bulbous, and the low posteriolateral margins have spread out over the fifth sternite.

Affinities and Distribution.—There can be little doubt of the affinity of the blind crayfish of Indiana with those of the solution caverns of Kentucky. In fact, the blind crayfishes from the caves of Harrison and Crawford counties on the Ohio River are decidedly similar to the Mammoth Cave species with only an occasional smooth, spineless specimen. The underground waters of Orange, Washington

and Lawrence counties a few miles to the north have populations of blind crayfish which are truly transitional between the species and subspecies. Smoothness, spine reduction and other *inermis* characteristics reach a climax in the cave populations in Monroe, Brown, and Bartholomew counties on the northern border of the range.

REFERENCES

COPE, E. D. 1871—Life in Wyandotte Cave. Indianapolis Journal, Sept. 5, 1871.

———1871—Life in Wyandotte Cave. Ann. and Mag. Nat. Hist. 4th ser., **8**(47):368-370.

———1872—On the Wyandotte Cave and its Fauna. Amer. Nat. **6**(7):406-422, fig. 116.

CREASER, E. P. 1933—Description of some New and Poorly Known Species of North American Crayfishes. Occ. Pap. Mus. Zool. Univ. Mich. **275**:1-21, pls. I-II.

ERICHSON, E. F. 1846—Übersicht den Arten der Gattung Astacus. Arch. f. Naturges. **12**(1):86-103.

FOWLER, H. W. 1912—The Crustacea of New Jersey. Ann. Rept. New Jersey Mus. 1911(2):31-650, pls. 1-150.

HAGEN, H. 1872—The Blind Crayfish. Amer. Nat. **6**(8):494-495.

HAY, W. P. 1893—Observations on the Blind Crayfishes of Indiana, with a Description of a New Subspecies; *Cambarus pellucidus testii*. Proc. U. S. Nat. Mus. **16**(935): 283-286, 2 pls.

HOBBS, H. H., JR. 1942—A Generic Revision of the Crayfishes of the Subfamily Cambarinae (Decapoda, Astacidae) with the description of a New Genus and Species. Amer. Midl. Nat. **28**(2):334-357, pls. 1-3.

PACKARD, A. S., JR. 1872—On the Cave Fauna of Indiana. Ann. Rept. Peabody Acad. Sci. **5**:93-97.

RHOADES, R. 1941—Notes on Some Crayfishes from Alabama Caves, with the Description of a New Species and a New Subspecies. Proc. U. S. Nat. Mus. **91**(3129):141-148, 2 fig.

TELLKAMPF, T. G. 1844—Über den blinden Fisch der Mammuthohle in Kentucky. Arch. f. Anat., Physiol., u. Med **4**(4):381-394, pl. IX.

An Analysis of the Feeding Habits of Rana p. pretiosa in Yellowstone Park, Wyoming[1]

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Knowledge of the food and feeding habits of the western spotted frog has been primarily based on the reports of Tanner (1931), Fitch (1936), Schonberger (1945) and Moore and Strickland (1955). These analyses have all been purely qualitative in nature and based on collections made at one time during the spring or summer.

The following study is based on an analysis of the contents of the digestive tracts of 178 individuals collected from populations in Yellowstone Park, Wyoming, during 1953, 1954, and 1955. Thirty-five of these frogs were collected on August 17, 1953, about one-half mile northeast of Fishing Bridge along a backwater of the Yellowstone River. The remainder of the sample was collected in 1954 and 1955 from other populations near the north end of Yellowstone Lake. Because the sample represents all age groups and was collected gradually over the course of several seasons it has been possible to learn something of seasonal variation (both qualitative and quantitative) in the diet of the western spotted frog.

Acknowledgment.—The writer wishes to acknowledge the role of members of the United States National Park Service in Yellowstone National Park, Wyoming, without whose cooperation this study could not have been carried out. Collection of materials was in accordance with a Class B permit. Appreciation is also expressed for use of facilities of the Museum of Vertebrate Zoology, and the Department of Zoology, University of California. In connection with the identification of materials recovered from the guts of frogs the writer wishes to gratefully acknowledge the assistance of the following persons: Dr. Paul D. Hurd, Jr., Assistant Entomologist, Department of Entomology and Parasitology, University of California, identified dipterans, hymenopterans, lepidopterans, and orthopterans (as well as certain representatives of other smaller groups); Hugh Leech of the California Academy of Science, identified both adult and larval beetles and certain other larvae; Dr. Willis Gertsch of the American Museum of Natural History identified the spiders; Dr. Robert Usinger, Department of Entomology and Parasitology, University of California, and John Herring identified the hemipterans; Dr. Donald Denning of Velsicol Corporation identified the trichopterans; Dr. Edward L. Bousfield identified the amphipods; Ernest Roscoe identified the snails; and Helen Sharsmith of the University of California Herbarium identified certain plant remains. Finally, it is a pleasure to acknowledge the assistance and direction of Dr. Robert C. Stebbins in the preparation of this manuscript.

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[1] This paper is extracted from the author's doctoral dissertation submitted at the University of California, Berkeley. Part of the preparation of the paper for publication was done while the author was on the staff at Wayne State University.

A contribution from the Museum of Vertebrate Zoology, Berkeley, Calif.

Feeding Behavior

Feeding is apparently carried on almost exclusively during the day or at dusk. During the early part of the season (May and June) this may be a more or less passive procedure, the frogs availing themselves of aquatic arthropods or insects and spiders encountered immediately adjacent to streams or ponds.

In July and August (and into September) the frogs devote more time and energy to securing prey and may range some distance from water in search of food. On July 25, 1954, at 2:50 p.m., I captured a male *Rana pretiosa* in an area grown with rank grasses and *Potentilla* some 40 feet from the banks of a stream. Part of a dioptid moth (*Gnophaela* sp.) protruded from the frog's mouth. On August 8, 1955, at 12:20 p.m., I found a frog in heavy grass with a grasshopper (*Trimerotropis* sp.) in its mouth. Finally, on August 19, 1955, at 2:30 p.m., I collected an adult female frog in the process of swallowing a large dragonfly (*Libellula saturata*).

On August 15, 1955, protracted observations with field glasses were made on a group of frogs occupying a small pond. Between about 5:30 and 7:00 p.m. three frogs were observed capturing mayflies and other insects at the surface of the pond and at its periphery. One frog seized a male lodgepole pine cone but spit it out. Perhaps it is significant that the frogs occupying this pond were almost exclusively crepuscular in their feeding activity while the frogs foraging away from the water were active at midday and during the afternoon. Certainly insects were more evident over the water of the pond at dusk than during the day.

Kilby (1945) working with *Rana pipiens* in Florida found that feeding occurred day and night as hunger and opportunity dictated, and Hamilton (1948) working in New York found that *Rana clamitans* fed at night. However, it is likely that the cold nights in the vicinity of Fishing Bridge inhibit nocturnal activity of both *Rana pretiosa* and the prey utilized by this frog in this section of Yellowstone Park.

Quantitative Analysis of Stomach Contents

In order to investigate possible variation in amount of food ingested during a summer season a quantitative analysis of the stomach, intestinal, and rectal contents of 112 frogs was carried out. The contents of the complete gut were removed from freshly killed frogs and preserved in weak (3-5 percent) formalin. Frogs were killed within 6 hours after capture.

The gut contents were introduced onto watch crystals and air-dried for from 2 to 4 days. The watch crystals and their contents were then weighed with a triple beam balance which was accurate to within about .02 grams. An average of two weighings was taken. Following these weighings rocks discernible with the unaided eye were extracted from the dried contents and weighed. The net weight of the contents

was determined by subtracting the weight of rocks, if any, from the dry weight.

The net weights ranged from 0 to 577 milligrams. Since a direct comparison of weights cannot be made except between frogs of the same size, it is difficult to work out the nature of seasonal variation in amount of ingested food in detail. However, in Table I an arrangement of the data is presented which demonstrates several points. Evidently, until the middle of June feeding is light. During July and early August it reaches, essentially, its peak. Maximal growth occurs in July and coincides with the apparent vigorous feeding initiated in that month. An extension of the sampling into September would reveal a decrease in amount of ingested food, but apparently the last half of August is marked by foraging as effective as that during July.

QUALITATIVE ANALYSIS OF STOMACH CONTENTS

The gut contents of 178 frogs were examined to discover the types of food utilized and variation in these types throughout the summer season. Thirty-six individuals contained no recognizable remains. More or less intact food items and large fragments were removed from the preserved gut contents and pinned in conventional manner or preserved in 70 percent alcohol. In the course of the field work intact specimens of snails, amphipods, and insects which had already been noted in stomachs or which were suspected to be likely food items were collected. In some instances these specimens enabled identification of fragments or distorted specimens.

Animal material.—Table II lists the recognizable animal food items recovered. Where fragments or parts clearly indicated the existence of a food item (e.g. recognizable head capsules, elytra, grasshopper femora or tibiae, etc.) the item has been counted. No attempt was made to infer presence either from dipteran or hymenopteran

TABLE I.—Seasonal changes in mean net weight of gut contents of 3 size-groups of *Rana p. pretiosa* in Yellowstone Park, Wyoming

	Date of collection of frogs											
	May 21-June 15			June 16-July 11			July 12-August 14			August 15-August 31		
Size range of frogs (mm)	N	Mean size of frogs (to ½ mm)	Mean net weight of gut contents (mg)	N	Mean size of frogs (to ½ mm)	Mean net weight of gut contents (mg)	N	Mean size of frogs (to ½ mm)	Mean net weight of gut contents (mg)	N	Mean size of frogs (to ½ mm)	Mean net weight of gut contents (mg)
25-42.5	6	31	16.5	5	33.5	14.2	8	35.5	26.9	20	35	32.0
43-59.5	5	55.5	24.2	5	55.5	74.2	24	53	137.9	12	48.5	59.8
60+	3	61	87.0	7	69.5	155.9	7	66.5	218.0	10	65.6	222.8

TABLE II.—Animal remains identified from the guts of 142 *Rana p. pretiosa* from Yellowstone Park, Wyoming

	Number of frogs containing item	Number of items
Mollusca		
Gastropoda		
Lymnaeidae		
Lymnaea palustris	4	10
Physidae		
Physa	1	2
Arthropoda		
Crustacea		
Gammarus lacustris	5	16
Arachnida		
Acarina		
Mite	1	1
Araneida		
Gnaphosidae		
Zelotes subterraneus	1	1
Linyphiidae		
Erigone denticulata	1	1
Pityohyphantes cristatus	1	1
Argiopidae		
Araneus patagiatus	2	2
Collinsia uta	1	1
Thomisidae		
Xysticus ferox	1	1
Philodromus alascensis	2	2
Thanatus coloradensis	1	1
Clubionidae		
Clubiona trivialis	1	1
Lycosidae		
Pirata piraticus	3	3
Tarentula aculeata	1	1
Tarentula	1	1
Trochosa terricola	1	1
Pardosa tetonensis	1	1
P. fuscula	1	1
P. coloradensis	1	1
P. concinna	1	1
Other *Pardosa*	1	1
Unidentified spiders	7	9
Insecta		
Thysanura		
?*Lepisma*	1	1
Collembola		
Isotoma	1	1
Orthoptera		
Acrididae		
Melanoplus	3	5
Trimerotropis	3	4
Tetrigidae		
Paratettix	1	1
Unidentified grasshoppers		
adults	5	6
nymphs	1	2
Neuroptera		
Mantispidae	1	1
Odonata		
Libellulidae		
Libellula saturata	1	1
Coenagrionidae		
adults	3	5
nymphs	2	2
Unidentified nymph	1	1
Plecoptera		
Pteronarcidae		
?*Pteronarcys*	1	1
?*Acroneuria*	1	1
Unidentified naiads	2	2
Hemiptera		
Corixidae		
Cenocorixa	1	1
Unidentified adult	1	1
Gerridae		
Gerris gillettei	15	28
G. notabilis	2	2
Miridae		
Lygus nymph	1	1
Unidentified adult	1	1
Nabidae		
Nabis ferus	1	1
Corizidae		
Corizus	4	4
Pentatomidae		
Peribalus limnolarius	2	2
Scutelleridae		
Eurygaster alternatus	2	3
Unidentified adults	2	2
Reduviidae		
Zelus nymph	1	1
Homoptera		
Cicadellidae	2	2
Fulgoridae		
Unidentified nymphs	1	2
Coleoptera		
Cicindelidae		
Cicindela longilabris	1	1
Carabidae		
Agonum	2	2
Amara	9	10
Bembidion	2	2
Calathus	2	2
Elaphrus	2	2
Pterostichus	6	6
Unidentified	10	13
Haliplidae		
Haliplus ?*ungularis*	1	1
?*Haliplus* larva	1	1
Dytiscidae		
Agabus strigulosus	1	1
A. antennatus	1	1
A. erichsoni	1	1
A. confinis	1	1
Other *Agabus*	1	1

TABLE II (*continued*)

	Number of frogs containing item	Number of items
Colymbetes	1	1
Hygrotus impressopunctatus	3	3
Hydroporus	1	1
Dytiscus ?dauricus larva	1	1
Agabus larva	1	1
Unidentified larva	1	1
Hydrophilidae		
Cercyon	2	2
Crenitis	1	1
Helophorus	4	4
Hydrobius fuscipes	1	1
Laccobius	2	2
Laccophilus ?decipiens larvae	1	2
Unidentified larva	1	1
Staphylinidae		
Oxytelus	1	3
Philonthus	3	3
Quedius	2	2
Unidentified	2	3
Cantharidae		
Podabrus	4	5
Cytilus alternatus	1	1
Cephaloidae		
Cephaloon	1	1
Elateridae		
Ctenicera and *?Ctenicera*	8	8
Horistonotus	3	3
?Dalopius	1	1
Unidentified adults	3	7
Unidentified larva	1	1
Elmidae		
Narpus solutus	1	1
Unidentified	1	1
Heteroceridae		
Heterocerus	3	3
Helodidae		
Cyphon	1	1
Coccinellidae		
Coccinella transversoguttata	4	4
?Hyperaspis	1	1
Scarabeidae		
Aphodius opacus	2	2
Dichelonyx	3	3
Cerambycidae		
Anoplodera chrysocoma	1	3
Chrysomelidae		
Trirhabda	9	21
Donacia	9	20
Phyllotreta	1	1
Altica	1	1
Galeruca	2	2
Unidentified larvae	2	3
Curculionidae		
Brachyrhinus ovatus	25	146
Calendra	1	2
Sitona	2	2
Unidentified adults	7	8
Scolytidae		
Hylurgops	1	1
Ips	1	1
Trichoptera		
Limnephilidae		
Limnephilus occidentalis	1	3
L. spinatus	1	2
Other *Limnephilus*		
Adults	2	2
Pupa	1	1
Cases and larvae	1	1
Lenarchus	1	1
Unidentified adults	3	3
Unidentified cases	3	3
Lepidoptera		
Dioptidae		
Gnophaela	1	1
Phalaenidae		
Unidentified adults	4	4
Unidentified larva	1	1
Lycaenidae		
Glaucopsyche	1	1
Unidentified larvae	5	9
Diptera		
Tipulidae	6	7
Chironomidae		
Chironomus	1	1
Unidentified larvae	5	many
Mycetophilidae		
Bolitophila	1	1
Exechia	1	1
Bibionidae		
Bibio	2	2
Stratiomyiidae		
Stratiomys	2	2
Eulalia	1	6
Tubifera maggot	1	1
Unidentified larvae	3	4
Therevidae		
Thereva and *?Thereva*	2	2
Dolichopidae		
Dolichopus	1	1
Empidae	3	3
Phoridae	3	6
Pipunculidae		
Pipunculus	2	2
Lonchaeidae		
Lonchaea	1	1
Ceratopogonidae	1	1
Syrphidae		
Syrphus	1	1
Metasyrphus	2	2
Criorrhina	1	1
Microdon	1	1
Unidentified	3	3

TABLE II (*continued*)

	Number of frogs containing item	Number of items		Number of frogs containing item	Number of items
Cordiluridae			*Muscina*	1	2
Cordilura	20	35	Unidentified larva	1	1
Helomyzidae			Hymenoptera		
Neoleria	1	1	Tenthredinidae		
Ephydridae			*Tenthredo*	1	1
Ephydra	4	4	*Rhogogaster*	1	1
Anthomyiidae			Sawfly larvae	11	18
Pegomya	1	1	Braconidae	3	4
Lispoides	4	4	Ichneumonidae		
Lispocephala	1	1	*Amblyteles*	3	3
Morellia	1	1	Unidentified adults	3	3
Hylemya	1	1	Gasteruptiidae		
Unidentified adults	3	4	*Aulacostethus*	2	2
Unidentified pupa	1	1	Platygasteridae	1	1
Calliphoridae			Formicidae		
Eucalliphora	2	2	*Camponotus*	10	11
Calliphora	3	3	*Formica*	16	19
Callitroga	1	1	*Lasius*	7	11
Sarcophagidae			Unidentified	39	88
Sarcophaga	1	2	Vespidae		
Senotainia	1	1	*Vespula vulgaris*	1	1
Tachinidae			*Ancistrocerus*	2	2
Fabriciella	1	1	Megachilidae		
Gonia	1	1	*Megachile*	2	2
Zenilla	1	1	*Osmia*	1	2
Muscidae			*Hoplitis clypeata*	1	1
Pyrellia	1	1			

wing fragments or from the various body fragments. Hence the listing is not to be construed as complete, but rather as a sample of animal prey ingested. Because of the longer persistence and easier recognition of coleopterous fragments the relative number of beetles is higher than it would have been had all items been equally persistent and recognizable.

The spectrum of utilized food items is quite broad, but the major groups involved as prey could have been predicted from a consideration of earlier studies. Moore and Strickland (1955) found an earthworm in one stomach of *Rana p. pretiosa;* this is the only major group of animals mentioned in earlier work not represented in the sample under consideration. In the present study, as well as in previous ones, it has developed that spiders and representatives of four orders of insects constitute from around 70 to 90 percent of all food items; it is of particular interest that in the Yellowstone study, 439 of the 802 recorded items (55 percent) are included in only 6 families of insects (Carabidae, Chrysomelidae, Curculionidae, Formicidae, Cordiluridae, and Gerridae).

An analysis of 36 prey species (or general types) utilized most commonly has been made in order to investigate possible differences

in feeding habits related to sex of frogs, time of season, or the ecological conditions existing in the various populations sampled.

There are no significant differences in feeding habits related to sex. However, the time of season, besides governing the amount of food ingested, apparently influences the species composition of the utilized food. In Table III the seasonal distributions of 13 prey species are summarized.

In general almost all beetles tend to be represented in stomachs more commonly during the latter part of the summer. A notable exception is the carabid *Pterostichus* which is taken from May until the end of August. Also some of the smaller water beetles (e.g. *Hygrotus*) may be consumed during the early part of the summer. Many forms are entirely absent from stomachs until late in the summer at which time they may be taken in appreciable numbers (e.g. sawfly larvae, lepidopteran larvae, grasshoppers). The dipteran genus *Cordilura* is represented by several species, some of which are among the few flying insects present in May. These flies may be eaten at this time. A large number of cordilurid flies is also consumed in August and this is associated with the emergence of another species of this fly. Other flies, hymenopterans, and hemipterans are more commonly consumed in July and August. *Gammarus* and caddis-fly larvae apparently are utilized only early in the season when the frogs are more closely restricted to the water. Adult trichopterans are eaten later in the summer after hatching. Some important prey species are available throughout the season. Besides *Pterostichus,* spiders and ants may be included in this category.

TABLE III.—Seasonal distribution of 13 selected types of prey utilized by 112 *Rana p. pretiosa* in Yellowstone Park, Wyoming. The first number represents the number of stomachs containing the organism, the second number represents the total number of that organism in all stomachs.

Organism	May 21-31	June 1-15	June 16-30	July 1-15	July 16-31	August 1-15	August 16-31
Gammarus lacustris	4-12		1-4				
Trichoptera, larvae and cases	5-5	1-1		1-1			
Hygrotus impressopunctatus	2-2			1-1			
Brachyrhinus ovatus			4-50	9-43	5-21	3-5	4-27
Donacia			2-7	1-1	4-10	1-1	1-1
Trichoptera, pupae and adults			1-3		1-1	1-1	4-7
Amara				2-2		1-1	6-7
Sawfly larvae					1-2	6-8	4-8
Cordilura	2-3	1-1		1-1		5-8	11-22
Pterostichus	1-1		1-1	1-1	2-2		1-1
Formica	1-1		3-3	1-1	3-5	8-9	
Camponotus	1-1			2-2		3-3	4-5
Trirhabda	1-1				1-2	2-8	5-11

The ecological conditions under which the four sampled populations exist may, in a few instances, influence the type of food consumed by frogs. For example, of 25 frogs that had consumed the strawberry crown-girdler (*Brachyrhinus ovatus*), 18 were taken from the vicinity of some small lakes, and 7 from other areas. Of 15 frogs that had eaten *Gerris gillettei,* 12 were from a stagnant backwater of the Yellowstone River and three from near the lakes. The snail *Lymnaea palustris* was represented in 3 frogs from near the lakes and one frog from the backwater. The abundance of the strawberry crown-girdler in the vicinity of the lakes may be associated with the fact that wild strawberry (*Fragaria virginicum*) is common there. Certainly this plant is not found in the open, almost marshy situations that occur adjacent to the Yellowstone River. On the other hand the quiet water of the lakes and backwaters of the river favor *Gerris* and *Lymnaea* while these animals are rarely encountered in streams.

The size relation of frogs and their prey is an important factor governing consumption of food. As Hamilton (1948) has pointed out, investigators have generally concluded that any animal small enough to be seized and swallowed may provide food for a frog. As will be seen, however, it is not necessarily true that the average size of food items consumed increases as the size of the frog increases. Representatives of almost all the prey species were measured (maximum dimension) with dial calipers and these "sizes" have been used in comparing sizes of frogs and their prey. The smallest recognized food items were certain tiny flies and wasps (e.g. platygasterids, phorids, *Dolichopus* and *Lonchaea*). Beetles only three millimeters in length were not uncommon (e.g. *Altica, Phyllotreta, Cercyon, Cyphon,* and *Crenitis*). The largest recovered food items were adult grasshoppers (*Trimerotropis* and *Melanoplus*) about 24 mm in length and the dragonfly *Libellula saturata* (54 mm). Table IV illustrates an analysis of 472 food items as related to the size of the predator.

As can be seen the smallest frogs eat only the small prey but large frogs consume items of considerable range in size. The largest prey is, of course, available only to the larger frogs. What is important to note is that about 75 percent of all items considered were between 4

TABLE IV.—Relationship of size of *Rana p. pretiosa* to size of ingested prey species in Yellowstone Park, Wyoming. Body of table indicates number of specimens of given size recovered from frogs of various sizes.

Size of frog (mm)	Sizes of prey items (mm)					
	2-3.5	4-5.5	6-9.5	10-13.5	14-17.5	18+
20-30.5	6	2	4			
31-40.5	5	19	25		1	
41-50.5	13	9	27	15		1
51-60.5	4	53	60	12	2	8
61-70.5	5	82	26	13	4	8
71+	1	42	15	7	1	2

and 9.5 mm in maximum dimension and the great majority of the food of all frogs more than 30 mm in length tends to fall within these limits. In other words, while frogs more than 50 mm long are capable of ingesting large prey items, they still take most of their food from smaller size classes. The size limits of 4 to 9.5 mm embrace about two-thirds of the prey species (and almost all the heavily utilized forms such as *Brachyrhinus, Cordilura, Trirhabda, Donacia, Amara, Camponotus, Formica,* etc.) but whether these forms are consumed because they are commoner or because they are of preferred size, I cannot say.

Representative prey animals in the size groups shown in Table IV are as follows:

2-3.5 mm — platygasterids, phorids, *Hylemya, Laccobius, Altica, Phyllotreta, Crenitis, Lasius, Helophorus, Dolichopus.*

4-5.5 mm — *Corizus, Trirhabda, Brachyrhinus, Camponotus, Formica.*

6-9.5 mm — *Amara, Coccinella, Donacia, Cordilura.*

10-13.5 mm — *Pterostichus, Gerris gillettei.*

14-17.5 mm — *Anoplodera chrysocoma, Criorrhina, Stratiomys, Cicindela longilabris, Pteronarcys.*

18 mm or larger — *Melanoplus, Trimerotropis, Libellula, Gnophaela, Gerris notabilis.*

Plant material.—Plant material in the digestive tracts of *Rana p. pretiosa* has been reported by Tanner (1931) and Schonberger (1945). In Yellowstone such material is common in stomachs, especially small objects up to about 10 mm in length. The two most commonly encountered items were male cones of *Pinus contorta* and the bract-like perigynia of sedges. Both structures often fall upon the water and could be seized at the moment of falling or ingested with other food items. In the stomachs of frogs that had been feeding on spent chironomids, perigynia were common, ingested along with the midges. The seizure of a male pine cone by a frog has already been described though in this instance the cone was rejected. Other vegetable material recovered included: 2 portions of needle fascicles of *Pinus contorta,* 1 fragment of a needle of *P. contorta,* 1 piece of wood 20 x 2 x 4 mm, various seeds, sections of sedge leaves, blades of grass, fragments of aquatic mosses, and a few fragments of various dicotyledons.

Rocks and dirt.—This sort of debris occurred in almost all stomachs if appreciable food material were present. Often it was impossible to distinguish dirt from organic remains. Rocks apparent to the unaided eye were removed and weighed. These occurred in 24 stomachs (from 1 to 11 in number, with an average of about 3) and the total weight ranged from less than 10 milligrams to 1,410 milligrams (median about 20 mg). The rocks were primarily obsidian, quartz and rhyolite. All these stones were small enough to be easily passed with the feces, except one. This rhyolite rock weighed 1,410 milligrams and was removed from the pyloric region of the stomach of an adult male frog. Its position was such that it occluded the pyloric

sphincter and prevented movement of food from the stomach to the duodenum. Both Drake (1914) and Kilby (1945) concluded that such materials are accidentally ingested by frogs. Kilby points out that such materials were not found in the stomachs of unfed frogs kept in an aquarium though rocks and sand were available.

FOOD HABITS OF LARVAE

A few observations of feeding by *Rana pretiosa* tadpoles were made, but when the intestinal contents of large tadpoles were examined, no recognizable remains could be found. At certain pools, the water starwort, *Callitriche palustris,* is present to the virtual exclusion of other plants during most of the summer, and tadpoles were often observed nibbling on this. *Spirogyra* is similarly utilized. Some time before transformation the *Callitriche* dies and pools are usually devoid of evident plant life during the latter stages of the tadpoles' development. I do not know on what the larvae subsist at this time. Burke (1933) has performed some interesting experiments with the tadpoles of *Rana p. pretiosa* which may shed some light on this problem. He found that the larvae were able to subsist, grow and transform (though slowly) when only bacteria from agar slants were present in the water. Controls from the same eggs kept in tap water starved in 2 to 3 weeks. Possibly bacteria may serve as a food source for tadpoles when natural vegetation is absent or much depleted.

DISCUSSION

One puzzling feature of analyses of anuran diets centers around the question of whether particular food items are actually chosen over others. Kilby (1945), who carried out an exhaustive study of the food habits of *Hyla c. cinerea* and *Rana pipiens* in Florida, has concluded that the prey consumed is governed largely by availability. In general the preceding data support this contention.

Several facts may be cited in support of the "availability" theory. For example on June 20, 1955, I collected 6 frogs from a lagoon adjacent to Yellowstone Lake. At the time the surface of the lagoon was covered with innumerable spent chironomids. The stomachs and rectums of the frogs collected were bulging with these insects. Various prey species are obviously utilized as they appear during the summer, as has been shown. Furthermore, certain forms (e.g. snails and water striders) are not available to all populations but they are eaten in areas where they are present. Hence, if selectivity exists, there can hardly be an inflexible scale of preference, for all populations do not have the same types of prey available. One would have to assume that preferences, if existent, have evolved along with the community itself. From a theoretical standpoint it would be disadvantageous to feed in accordance with a rigid pattern of selectivity. Arthropod species are particularly susceptible to fluctuations in numbers, and an animal with plastic

feeding patterns would thus be able to subsist on whatever happened to be available. On the other hand, while *Gammarus* may be consumed in May when there is probably a paucity of available food, later in the season it is ignored though still available. Here, however, a change in the habits of the frogs is involved too.

Thus, while food habits may appear to reflect a simple, opportunistic seizure of available types, some sort of preference may exist though undemonstrable except by repeated quantitative samplings of the habitat coincidentally with the acquisition of stomach samples. Certainly we know little concerning insects that are possibly repugnant to frogs for, in the absence of sampling, such forms could well go undetected. Hamilton (1948) has stated that: "It appears improbable that this factor is actually effective under natural conditions. Stink bugs of various species are frequently eaten by the green frog." In the absence of some sort of quantitative sampling, this assumption is unjustified. Cott (1934) has pointed out that some amphibians do actually refuse certain items of food though these may be made available repeatedly.

A minor question raised by both Kilby (1945) and Hamilton (1948) concerns whether *Rana pipiens* and *Rana clamitans* feed under water. Both authors concluded that on the basis of certain stomach contents, e.g., fish, crustaceans, etc., these frogs must at least capture some prey under water. The presence of *Gammarus,* trichopteran, odonatan and other aquatic insect larvae and nymphs in the stomachs of *Rana p. pretiosa* indicates that the spotted frog also feeds under water.

REFERENCES

BURKE, V. 1933—Bacteria as food for vertebrates. Science **78**(2018):194-195.

COTT, H. B. 1934—Relative acceptability. Proc. Ent. Soc. London **9**:31-34.

DRAKE, CARL J. 1914—The food of *Rana pipiens* Schreber. Ohio Nat. **14**: 257-269.

FITCH, HENRY S. 1936—Amphibians and reptiles of the Rogue River Basin, Oregon. Amer. Midl. Nat. **17**(3):634-652.

HAMILTON, W. J., JR. 1948—The food and feeding behavior of the green frog, *Rana clamitans* Latreille, in New York state. Copeia **1948**(3):203-207.

KILBY, JOHN D. 1945—A biological analysis of the food and feeding habits of two frogs, *Hyla cinerea* and *Rana pipiens sphenocephala.* Quart. Jour. Fla. Acad. Sci. **8**:71-104.

MOORE, J. E. AND E. H STRICKLAND 1955—Further notes on the food of Alberta amphibians. Amer. Midl. Nat. **54**(1):253.

SCHONBERGER, C. F. 1945—Food of some amphibians and reptiles of Oregon and Washington. Copeia **1945**(2):120-121.

TANNER, VASCO M. 1931—A synoptical study of Utah Amphibia. Contr. Dept. Zool. and Ent. Brigham Young Univ. No. 40. Utah Acad. Sci. **8**:159-198.

The Distribution of Some Mississippi Lizards

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The Department of Biology Museum, Mississippi Southern College, contains approximately 500 specimens of lizards from Mississippi, principally from the southeastern part of the state. Twelve species and subspecies are represented. Distributional data and other pertinent information based on this material are now presented. A few specimens in the collection of the Perkinston (Mississippi) Junior College (now destroyed by fire) are included in the report.

There have been few published works dealing with the herpetofauna of Mississippi (Potter, 1920; Smith and List, 1955); the majority have dealt principally with the three coastal counties (Allen, 1932; Brimley, 1920; Corrington, 1927; and Ward *et al.,* 1953). The most extensive investigations of lizards in the state are recorded by Cook (1943). Scattered references to lizards from Mississippi are made by several authors (Burt, 1931; Cope, 1900; Smith, 1946; Smith and Smith, 1952; and Taylor, 1935). Some of the older literature references to anonymous specimens of *Ophisaurus, Eumeces,* and *Sceloporus* are relatively useless because of changes in nomenclature.

In the following account, new county records are indicated by an asterisk *.

Anolis carolinensis carolinensis Voigt.—(103 specimens).

Copiah Co.: 4 mi. E. Hazlehurst. **Covington Co.*: 5 mi. NW. Collins (5); 1 mi. NE. Collins. *Forrest Co.*: Hattiesburg (18); Petal (2); 8 mi. SE. Hattiesburg (2); 12 mi. SE. Hattiesburg; 12 mi. S. Hattiesburg; 14 mi. S. Hattiesburg; 4 mi. N. Hattiesburg (4); 6 mi. N. Hattiesburg (10). *Hancock Co.*: Clermont Harbor (2); Edwardsville (10). *Harrison Co.*: Bayou Bernard, Gulfport (4). *Jackson Co.*: Pascagoula (4); Daisy-Vestry; Horn I. **Jasper Co.*: 3 mi. E. Louin (4); 8 mi. NW. Heidelberg (3). *Jones Co.*: Laurel (2). **Lamar Co.*: 1 mi. W. Hattiesburg; 6 mi. W. Hattiesburg (3); 9 mi. W. Hattiesburg; 12 mi. W. Hattiesburg; 8 mi. SW. Hattiesburg. *Pearl River Co.*: 13 mi. S. Poplarville (2). **Perry Co.*: New Augusta (3); 3 mi. S. New Augusta (6); Richton. **Simpson Co.*: Saratoga (2). **Smith Co.*: 1 mi. E. Mize; 8 mi. N. Mize (2). **Wayne Co.*: 1 mi. W. Waynesboro. **Wilkinson Co.*: Centreville.

Sceloporus undulatus Latreille.—(170 specimens).

Copiah Co.: Henneberry Game Refuge, Barlow (3); 4 mi. E. Hazlehurst (15). **Covington Co.*: 1 mi. NE. Collins (3); 5 mi. NW. Collins (4). *Forrest Co.*: Hattiesburg and vicinity (11); Rawls Springs, 6 mi. NW. Hattiesburg (5); Hattiesburg Municipal Airport (6); 9 mi. SW. Hattiesburg; 6 mi. S. Hattiesburg (3); 12 mi. S. Hattiesburg; 15 mi. S. Hattiesburg (2); 8 mi. SE. Hattiesburg (2); 12 mi. SE. Hattiesburg; Eatonville, 6 mi. N. Hattiesburg. **George Co.*: 6 mi. N. Daisy-Vestry, near Black Creek (3). *Hancock Co.*: Clermont Harbor (5); Edwardsville (3). *Jackson Co.*: Moss Point (4); Gautier. **Jasper Co.*: 7 mi. SW. Bay Springs; 3 mi. E. Louin (6); 8 mi. NW. Heidelberg (2). *Jones Co.*: 7 mi. N. Laurel; NW. Laurel (3). *Kemper Co.*:

7 mi. S. Electric Mills. *Lamar Co.*: 12 mi. W. Purvis (17); 3 mi. SW. Hattiesburg (2); 8 mi. SW. Hattiesburg (2); 10 mi. SW. Hattiesburg (3); 6 mi. W. Hattiesburg (5); 7 mi. W. Hattiesburg (2); 8 mi. W. Hattiesburg (6); 9 mi. W. Hattiesburg; 10 mi. W. Hattiesburg. *Pearl River Co.*: 10 mi. W. Poplarville; 13 mi. S. Poplarville (2). **Perry Co.*: New Augusta; 3 mi. S. New Augusta (4); 1 mi. S. Richton (2). *Pike Co.*: 6 mi. E. McComb (2); 7 mi. E. McComb. *Rankin Co.*: 2 mi. S. Florence. *Simpson Co.*: Saratoga (9); 4 mi. S. Star (4). **Smith Co.*: 8 mi. N. Mize (4). *Stone Co.*: 5 mi. S. Wiggins; 15 mi. E. Perkinston (5). *Tishomingo Co.*: 5.3 mi. E. Tishomingo; Tishomingo State Park (2). *Wayne Co.*: 3 mi. W. Waynesboro (3).

According to Smith (1946:224), the southern fence lizard can be differentiated from the northern race by the following criterion: 92 percent of *undulatus* have 37 or less dorsal scales, and 95 percent of *hyacinthinus* have 38 or more.

There is a gradual reduction in the number of dorsal scales from north to south among our specimens. In Jackson County 92 percent of the specimens examined have 37 or less scales; 91 percent of those from Hancock County have 37 or less. In Kemper and Tishomingo counties more than 95 percent of the specimens examined have 38 or more dorsal scales. On this basis, all Mississippi *Sceloporus* studied are from intergrading populations, except those from the coast (*S. u. undulatus*) and those from Kemper County northward (*S. u. hyacinthinus*).

Phrynosoma cornutum Harlan.—(5 specimens).

**Forrest Co.*: Petal; Hattiesburg. **Hancock Co.*: Bay St. Louis area. **Stone Co.*: Big Level, E. Wiggins (2).

There is no evidence of a permanent colony of *cornutum* in the state. The Stone County specimens are the only ones found in a strictly rural area, removed from well-traveled roads or urban areas.

Ophisaurus ventralis Linnaeus.—(28 specimens).

Forrest Co.: Hattiesburg (8); 6 mi. S. Hattiesburg (2). *Hancock Co.*: Lakeshore (5); Bay St. Louis (3); W. of Bay St. Louis (2); Waveland. *Harrison Co.*: 7 mi. N. Biloxi. *Jackson Co.*: Vancleave; Gautier, 5 mi. W. Pascagoula; Gulf Coast Research Laboratory, Ocean Springs. **Jefferson Davis Co.*: Prentiss. **Perry Co.*: 1 mi. S. Richton (2).

Since other reports were dated prior to that of McConkey (1954), all *Ophisaurus* were referred to the species *ventralis*. According to McConkey, both *O. ventralis* and *O. attenuatus longicaudus* occur in the same locality, separated by habitat preferences, and both are state-wide in distribution. Consequently, without a re-examination of all specimens previously reported, it is not practical to accept the records at face value. These old records, although given as *O. ventralis*, may be retained only as *Ophisaurus* species.

McConkey, after describing the subspecies *O. a. longicaudus*, records the restricted species *ventralis* from Hancock, Harrison, and Lauderdale counties, in southeast Mississippi. Examination of our specimens of *Ophisaurus* in the light of McConkey's descriptions re-

veals *ventralis* to be more commonly taken in southeast Mississippi. Specimens, having no middorsal stripe or ventral stripes and with white markings at posterior corners of dorsal scales, are designated as *ventralis*. The latter character is not apparent in all adult specimens; some have no light markings. McConkey states that the markings may be absent only in very young individuals.

Ophisaurus attenuatus longicaudus McConkey.—(7 specimens).

**Covington Co.*: Lux Lake, 12 mi. N. Hattiesburg. **Forrest Co.*: 6 mi. S. Hattiesburg. **Lamar Co.*: 6 mi. W. Hattiesburg. **Lee Co.*: Tupelo. **Perry Co.*: 10 mi. N. New Augusta; US HW 98, SE. Hattiesburg. **Tishomingo Co.*: 2.5 mi. W. Burnsville.

Mississippi Southern College material having a middorsal stripe, ventral stripes, and with white markings in the centers of dorsal scales are designated as *longicaudus*. In some of these specimens, the dorsolateral white markings form narrow stripes. *O. a. longicaudus* has not been previously reported from any of the counties represented in the MSC collection. These records fill some of the gaps existing in the range of this form. The segregation of *ventralis* from *longicaudus* by habitat preferences may be more fancied than real. At any rate, MSC No. 55.69 includes two specimens taken simultaneously at the same spot; one is *ventralis* and the other is *longicaudus*. McConkey reports 36 *ventralis* and 6 *longicaudus* from Mississippi, a ratio of 6:1. In the MSC collection there are 28 *ventralis* and 7 *longicaudus* — a 4:1 ratio. These figures suggest that *ventralis* is by far the more common of the two forms.

Cnemidophorus sexlineatus Linnaeus.—(24 specimens).

**Covington Co.*: 1 mi. NE. Collins. **DeSoto Co.*: 2.7 mi. N. Walls. **Forrest Co.*: Hattiesburg; 5 mi. S. Hattiesburg; 12 mi. S. Hattiesburg; 6 mi. N. Hattiesburg. *Hancock Co.*: Bay St. Louis. *Jackson Co.*: Gautier; Gulf Coast Research Laboratory, Ocean Springs; Horn I. *Jones Co.*: 7 mi. N. Laurel (2). **Kemper Co.*: 7 mi. S. Electric Mills. *Lamar Co.*: 7 mi. W. Hattiesburg; 12 mi. W. Purvis. **Perry Co.*: Ragland Hills, US HW 98, SE. Hattiesburg; 3 mi. E. New Augusta (2). **Scott Co.*: 4 mi. S. Morton. **Simpson Co.*: Saratoga (2). *Tishomingo Co.*: Tishomingo State Park. **Walthall Co.*: near Tylertown; 11 mi. N. Tylertown.

Lygosoma laterale Say.—(69 specimens).

Copiah Co.: 4 mi. E. Hazlehurst. **Covington Co.*: 8 mi. NW. Collins (2). *Forrest Co.*: Hattiesburg and vicinity (7); 4-6 mi. N. Hattiesburg (2); 6 mi. S. Hattiesburg; 12 mi. SE. Hattiesburg (3). **Hancock Co.*: Clermont Harbor (5); NW. Bay St. Louis (2). *Hinds Co.*: E. Raymond. *Jackson Co.*: Pascagoula (9); Moss Point (7); 6 mi. W. Gautier; Vancleave (2). **Jasper Co.*: 7 mi. SW. Bay Springs (2); 8 mi. NW. Heidelberg (2); 3 mi. E. Louin. *Lamar Co.*: 7, 8, 9 mi. W. Hattiesburg (3); W. Oak Grove at Perkins Creek (4); SW. Oak Grove; 13 mi. SW. Hattiesburg (2). **Perry Co.*: 1 mi. S. Richton (2). *Pike Co.*: Fernwood; Percy Quin State Park. **Smith Co.*: 8 mi. N. Mize. **Tishomingo Co.*: SW. Iuka. *Wayne Co.*: 21 mi. E. Laurel (2). **Wilkinson Co.*: Centreville (3).

Eumeces fasciatus Linnaeus.—(31 specimens).

Claiborne Co.: S. Vicksburg at Big Black River, US HW 61. *Copiah Co.*: 4 mi. E. Hazlehurst. *Covington Co.*: 0.5 mi. NE. Collins (2). *Forrest Co.*: Hattiesburg and vicinity (6); 12 mi. S. Hattiesburg (2); 10 mi. N. Hattiesburg; Rawls Springs, 6 mi. NW. Hattiesburg. *Hancock Co.*: 2 mi. N. Logtown. *Issaquena-Sharkey* cos.: County line, US HW 61. *Jackson Co.*: Pascagoula; Moss Point; Vancleave ; 6 mi. W. Gautier. *Jones Co.*: 8 mi. E. Laurel. *Lamar Co.*: 5 mi. W. Hattiesburg; 7 mi. W. Hattiesburg (2); 12 mi. W. Purvis. *Perry Co.*: Beaumont; New Augusta; 1 mi. S. Richton (2). *Tishomingo Co.*: 5.3 mi. E. Tishomingo on Bear Creek. *Walthall Co.*: 14 mi. SW. Columbia.

Eumeces laticeps Schneider.

Forrest Co.: 2.5 mi. SE. Hattiesburg.

Eumeces inexpectatus Taylor.—(46 specimens).

**Copiah Co.*: 4 mi. E. Hazlehurst (2). **Covington Co.*: 5 mi. NW. Collins; 8 mi. NW. Collins. **Forrest Co.*: 14 mi. S. Hattiesburg; 5 mi. N. Hattiesburg (2); 2 mi. N. Hattiesburg; 3.5 mi. W. Rawls Springs; 8 mi. SE. Hattiesburg. *Hancock Co.*: Clermont Harbor; 4 mi. SE. Santa Rosa; Bay St. Louis. *Jackson Co.*: Pascagoula (16); Moss Point (2); 6 mi. W. Gautier (2). **Jones Co.*: 7 mi. N. Laurel. **Kemper Co.*: 7 mi. S. Electric Mills. **Lamar Co.*: 5 mi. (2), 6 mi. (1), 7 mi. (2) W. Hattiesburg; 12 mi. W. Purvis. **Lee Co.*: 8 mi. N. Tupelo. **Wayne Co.*: 21 mi. E. Laurel. **Webster Co.*: 3 mi. W. Eupora. **Wilkinson Co.*: Centreville (2).

Eumeces anthracinus pluvialis Cope.

**Lamar Co.*: 9.5 mi. W. Hattiesburg and 2 mi. S. Oak Grove at Perkins Creek.

REFERENCES

ALLEN, M. J. 1932—A survey of the amphibians and reptiles of Harrison County, Mississippi. Amer. Mus. Nov. **542**:1-20.

BRIMLEY, C. S. 1910—Records of some reptiles and batrachians from the Southeastern United States. Copeia **28**:9-18.

BURT, C. E. 1931—A study of the Teiid lizards of the genus *Cnemidophorus*, with special reference to their phylogenetic relationships. Bull. U. S. Nat. Mus. **154**:1-286.

COOK, F. A. 1943—Alligator and lizards of Mississippi. Miss. State Game and Fish Comm. Surv. Bull., Jackson, Miss. pp. i-v, 1-20.

COPE, E. D. 1900—The crocodilians, lizards, and snakes of North America. Rep. U. S. Nat. Mus. for 1898. pp. 153-1270.

CORRINGTON, J. D. 1927—Field notes on some amphibians and reptiles at Biloxi, Mississippi. Copeia **165**:98-102.

MCCONKEY, E. H. 1954—A systematic study of the North American lizards of the genus Ophisaurus. Amer. Midl. Nat. **51**:133-169.

POTTER, D. 1920—Reptiles and amphibians collected in northern Mississippi in 1919. Copeia **86**:82-83.

SMITH, H. M. 1946—Handbook of lizards. Comstock Pub. Co., Ithaca, N. Y. pp. i-xiv, 1-557.

SMITH, P. W. AND J. C. LIST 1955—Notes on Mississippi amphibians and reptiles. Amer. Midl. Nat. **53**:115-125.

——— AND H. M. SMITH 1952—Geographic variation in the lizard *Eumeces anthracinus*. Univ. Kans. Sci. Bull. **34**:679-694.

TAYLOR, E. H. 1935—A taxonomic study of the cosmopolitan lizards of the genus *Eumeces*, with an account of the distribution and relationships of the species. Univ. Kans. Sci. Bull. **23**:1-643.

WARD, J. W. ET AL. 1953—A list of animals collected in the area of the Mississippi Gulf Coast Research Laboratory at Ocean Springs, Mississippi, during the summer of 1947. Preliminary report no. 1. Jour. Miss. Acad. Sci. **4**:22-24.

A Quantitative Study of Mountain Beaver Activity

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Most of the articles on the habits of mountain beavers [*Aplodontia rufa* (Rafinesque 1817)] describe the animal as being chiefly nocturnal. Grinnell and Storer (1924) refer to it as "reclusive" and as one whose, "activity is confined to night time." Bailey (1936) and Seton (1929) similarly allude to the nocturnal activity and the last writer states, "he seems positively to dread the sunshine." In the Pacific Northwest, Scheffer (1929) believes the animal to be active in its burrows during the day time but that it never leaves the burrows except at night. More recently, however, Dalquest (1948) finds that although the mountain beaver is principally active at night, it is frequently seen during the day, especially in the fall. Because all of these published statements, except those of Dalquest (*op. cit.*) were at variance or inconsistent with this author's own field experience with the mountain beaver, the following observations and experiments were planned to investigate the nature of its activity.

Methods of Study

Observations have been made on three colonies near Huntington Lake, California, at 7000 feet elevation over the past 13 years. Although the colonies were visited weekly, chiefly during the summer months, a few visits were made after they were covered with deep snow in winter and early spring.

In August, 1957, a young female mountain beaver, weighing 450 grams, was live-trapped and placed in a small outdoor pen including 10 square feet of earth. A small wooden nest box and a water pan were provided. The pen was constructed near the site of the home colony where the animal could readily be observed during the day or night. The captive was provided with an abundance of its natural food and fresh water at all times. After the animal was observed for 27 days, it was marked and released at the site of the home colony.

In August, 1958, a steel-sided pen, enclosing 100 square feet of seepage, covered with natural vegetation, was constructed about 300 yards downstream from a colony. Two underground burrows and nests were made outside the pen and were connected to it by underground tile runways which were always partially filled with seepage water near their entrances. The living conditions in this pen were made to simulate as closely as possible those that prevailed naturally in the colony. Two female mountain beavers were live-trapped and kept in the pen for observation and experimentation. One of the animals was adult, and the other was about two-thirds grown.

The two animals were observed as they lived together for three

weeks. The adult was then marked and released. The activity of the younger animal was further studied for three more weeks before it, too, was marked and released. The activity of the final three weeks of this animal was studied by means of an electric recording apparatus. This apparatus consisted of a treadle-switch which was solidly anchored at the entrance of the burrow used by the animal. The treadle-switch was connected to a 12-volt storage battery which activated an electromagnet equipped with a sharp pencil. The pencil made a dot on a clock-driven circular disk of paper with each contact. The paper was marked off in 12 hour segments, each of which was divided into six 10-minute segments. During an activity period, the animal moved into and out of the burrow several times; it was easy to determine from the dots on the paper disk not only the time of exit and entrance, but also length of time occupied by any activity or rest period.

This recording apparatus was finally set in a natural underground runway with many openings in its roof, at the site of the colony for a period of one week. The runway was 55 yards long and ran parallel to a small stream. Both were thickly overgrown with vegetation. Freshly cut plants in the tunnel attested to its use by a mountain beaver (or beavers). An animal could emerge at any one of the many roof openings in the tunnel and feed at anytime unobserved because of the dense cover provided by willows, tall grasses and sedges.

RESULTS

Mountain beavers frequently have been seen at any hour of the day during the summer months at all three colonies. The animals were usually only a short distance from a runway and nearly always under the protective cover of heavy herbage or low-growing willows. Sometimes they were observed in the open either in bright sunshine close to their runways, or swimming, or walking across the little rivulets that cut through the areas occupied by the colonies. During the day they were rarely seen more than 20 feet from a burrow on their well-beaten surface trails through thick vegetation. These trails were frequently 75 yards or more in length.

The observations of the first captive (1957) revealed that the animal had regular periods of activity and rest. It was observed, also, that night or day, rain or shine, moon or moonless nights, made little, if any, difference in the regularity or length of these periods.

The 20 carefully studied periods of rest and activity for this animal did not differ from those recorded electrically for another animal (Table I) in 1958.

The same regularity of rest and activity periods was observed during a three-week period for the two animals (1958) which were kept together in the larger pen with its more natural conditions. They were usually active at different times, but they always occupied the same nest while at rest.

The results obtained with the electric recording apparatus for the young female (1958) are included in Table I and Figure 1.

The number of activity periods each day ranged from 6 to 7 for all three captive animals. The average for the young female whose activity was electrically recorded was 6.6 per day over the 18-day period. Except for a few records excluded, when the animal immediately re-entered the burrow after an exit, the length of an activity period ranged from a few seconds to one that was 2 hours and 45 minutes long. The data are summarized in Table I. By observing the animals daily, it was determined that practically all of the time of the animal's activity periods was spent in eating.

The coefficient or ratio of night-day activity was calculated by dividing the number of night contacts (7 p.m. to 7 a.m.) by those made during the day (7 a.m. to 7 p.m.). This was found to be 1.62 for the 18 days, which means the animal was somewhat more than half again as active at night as compared to the day time.

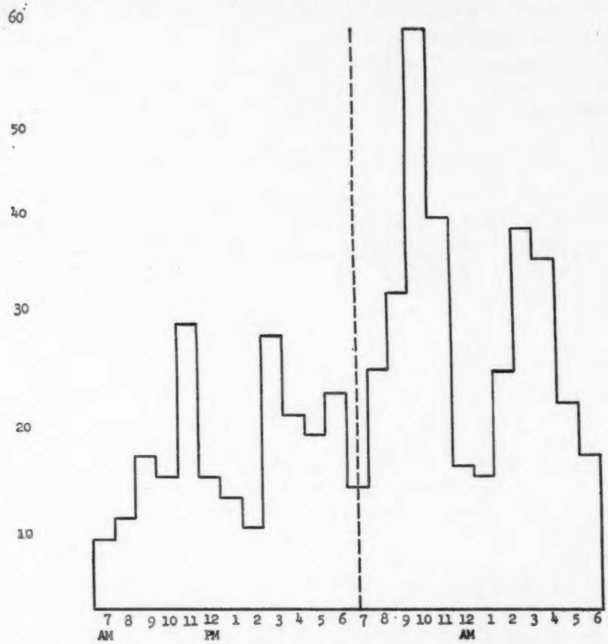

Fig. 1.—Activity periods of a female mountain beaver, electrically recorded for an 18-day period. Vertical numbers represent the number of 15-minute periods during which the animal was active for a particular hour during the 18-day study. The broken vertical line roughly separates "day" from "night" records.

The coefficient of activity (Szymanski, 1918) was found by dividing the number of 15-minute periods during which there was activity by those periods in which there was no activity. This was found to be 0.44 for the captive animal for the 18 days.

TABLE I. — Lengths of time in the periods of activity and rest for a captive mountain beaver for 18 days in summer

	NIGHT	DAY
Longest activity period	2 hrs., 45 mins.	2 hrs.
Average activity period (N-57, D-61)*	1 hr., 30 mins.	1 hr., 8 mins.
Longest rest period	3 hrs., 30 mins.	4 hrs., 15 mins.
Average rest period (N-71, D-71)*	2 hrs., 30 mins.	3 hrs., 10 mins.

* Total number of records used; N, night; D, day.

The records obtained on an animal (or animals) from a natural runway showed activity at nearly all hours of the day or night during the week the apparatus was set in one runway at the colony. The coefficient or ratio of night-day activity for this "wild" animal (or animals) was 1.53.

DISCUSSIONS AND CONCLUSIONS

Field observations, as well as experiments on captive animals, indicate the mountain beaver may be active outside its burrow at any hour during the night or day, however, there is 50 to 60 percent more activity at night. The data (see Fig. 1) indicate that the animal has 6 or 7 activity periods each 24 hours during the summer. The activity periods are mostly spent in feeding. The 18-day record of one animal showed these activity periods to be variable in length (Table I). They are grouped around four peaks which centered about 3 a.m., 11 a.m., 3 p.m., and 10 p.m. (Fig. 1). The activity peaks at 10 p.m. and at 3 a.m. are the largest. Just why this species should be more active at night is not known, since an abundance of food is immediately available under good protective cover at all times in summer. The activity of the animal (or animals) at the colony closely paralleled that of the captive animal (Fig. 1) and showed a comparable ratio or coefficient of night-day activity. This suggests that the species has greater activity at night. The greater nocturnal activity cannot be due to the absence of predators since the two most common potential enemies, the coyote (*Canis latrans*) and the horned owl (*Bubo virginianus*), are more active at night at the site of the colony.

Possibly the tendency to be more active at night may have become a part of this primitive rodent's pattern of behavior long ago under different conditions than those that now prevail. The greater nocturnal activity may actually be stimulated and initiated by the decreasing intensity of light, the drop in temperature, the rising relative humidity,

the down-mountain breeze, or combinations of these factors that prevail as night begins.

SUMMARY

Mountain beavers may be active and out of their burrows at all hours of the day or night. At night, they are more active and wander farther from their underground runways, which, even during the day, lead them to an abundance of protected feeding places.

There are 6 or 7 activity periods that occur with considerable regularity each 24 hours. These activity periods vary in length up to 2 hours and 45 minutes. They average 22 minutes longer at night. The activity periods of a captive animal grouped themselves about four activity peaks; the two periods at night being the largest. There is no explanation for the mountain beaver being more nocturnal than diurnal in summer since an abundance of food is safely available at all times.

REFERENCES

BAILEY, VERNON 1936—The Mammals and Life Zones of Oregon. North Amer. Fauna **55**:416; 52 pls.

DALQUEST, WALTER W. 1948—Mammals of Washington. Pub. Univ. Kas. Mus. Nat. Hist. **2**:1-444; 140 figs.

GRINNELL, JOSEPH AND TRACE I. STORER 1924—Animal Life in the Yosemite. Univ. Calif. Press, Berkeley. 669 pp. 60 pls.

SCHEFFER, THEO. H. 1929—Mountain Beavers in the Pacific Northwest: their habits, economic status and control. U S. Dept. Agric. Farmers' Bull. **1598**:1-18.

SETON, ERNEST THOMPSON 1929. Lives of the Game Animals, Vol. 4 (part II): 441-947, 113 pls. Doubleday Doran & Co. Inc., New York.

SZYMANSKI, J. S. 1918—Die Verteilung der Ruhe und Aktivitätsperioden bei weissen Ratten und Tanzmäusen. Arch. Ges. Physiol. **171**:324.

Seasonal Biotic Events in Two Colorado Alpine Tundra Ponds[1]

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The rugged terrain and the rigorous climatic conditions of the alpine tundra present a rather formidable picture to the field biologist. The long winter, deep snow, blizzards, and high winds make the alpine tundra relatively inaccessible for biological studies with ordinary equipment during much of the year. Even in the short summer, high winds, frequent cold showers, and summer blizzards are likely to occur at any time. It has long been generally recognized that such severe climatic conditions are remarkably restrictive upon the aquatic as well as the terrestrial biota of the tundra.

With the exception of Neldner and Pennak (1955), who conducted a full open season study on a single Colorado alpine pond, the American literature on tundra ponds is almost non-existent, being limited to brief descriptions, single visits, and casual observations. European investigators, such as Brink and Wingstrand (1949), Pesta (1933, 1935, 1943, 1948), Pichler (1939a, 1939b), Stirnimann (1926), Thomasson (1951, 1952), and Turnowsky (1946), have produced a much more extensive array of literature, but like the majority of American papers, these are brief descriptions and not full seasonal studies.

It is the purpose of the present paper to give a limnological description of two small Colorado alpine tundra ponds, based upon observations and data gathered at relatively frequent intervals during the entire open season. Some routine physical and chemical determinations were conducted, but special emphasis was placed upon the ecology of the benthic fauna and zooplankton, with little regard to the botanical aspect.

Acknowledgment. — I am especially indebted to Dr. Robert W. Pennak for the confirmation of many taxonomic determinations and criticism of the manuscript. I am also grateful to Mr. H. B. Herrington for species determination of fingernail clam specimens. I am further indebted to Mr. Robert P. Higgins for assistance in the field determination of pond morphometry.

Description of Ponds

Washboiler Pond (hitherto unnamed) and Dead Hat Pond (hitherto unnamed) are located in Summit County, Colorado, at 39° 40′ north latitude and 105° 52′ west longitude. The ponds are situated only 30 meters apart at an elevation of 3,582 meters (11,750 feet) in a glaciated valley at the southwest foot of Mount Sniktau on

[1] Contribution No. 35, Limnology Laboratory, Department of Biology, University of Colorado.

Fig. 1.—Dead Hat Pond (arrow, slightly left of center) as seen from U. S. Highway 6 at the summit of Loveland Pass.

the Continental Divide, well above timberline. Pennak (1941, 1958) suggests 3,200 meters elevation as the lower limit of the alpine limnological zone at this latitude. Dead Hat Pond can easily be seen from U. S. Highway 6 at the summit of Loveland Pass (3,656 meters), but Washboiler Pond is obscured from view by a small terminal moraine in the foreground (Fig. 1).

The alpine meadow in which the ponds are located lies in a valley surrounded on the west, north, east, and south by the summit of Loveland Pass, Mount Sniktau, Baker Mountain, and Lenawee Mountain, respectively. The valley was probably formed sometime in the late Wisconsin by the plucking action of a small glacier. The valley supports a typical alpine vegetation of which *Carex* spp., *Salix* sp., *Ranunculus* spp., *Sedum* sp., *Caltha* sp., and *Poa* sp. are examples.

Dead Hat Pond is located 30 meters east of Washboiler Pond, and both are roughly oblong in shape (Figs. 2, 3, 4, and 5). Washboiler Pond is about 2 by 6 meters with a maximum depth of 0.56 meters (Fig. 4). Dead Hat Pond is about 4 by 9 meters with a maximum depth of 0.50 meters (Fig. 5). Dead Hat Pond differs from Washboiler Pond in that it has a small northeast "bay" with a maximum depth of 0.24 meters, and a small island in its eastern half, which supports a small *Carex* growth.

The basins of both ponds are saucer-shaped, and receive drainage from melting snow banks on the north and west slopes, as well as water from showers, frequent in the alpine tundra. It may be noted that Dead Hat Pond probably receives a slight bit of drainage from the outlet of Washboiler Pond. The basins of these ponds should not

Fig. 2. — Washboiler Pond, looking south.

be confused with the staircase and thrust-pond types characterized by Ives (1941), but are merely saucer-shaped depressions in an alpine meadow.

Both Washboiler Pond and Dead Hat Pond possess drainage outlets on the north and east northeast sides, respectively (Figs. 4 and 5). Water-level fluctuations are common to both ponds during the summer months, especially after the snow banks have melted. However, frequent heavy showers and the resulting drainage periodically restore the ponds to their natural levels. The lowest maximum depth recorded during the open season was 0.3 meters in Dead Hat Pond on September 10.

The bottom deposits of Washboiler Pond and Dead Hat Pond are difficult to characterize. Bottom samples are black, mixed with decaying plant material, somewhat putrified, and emit hydrogen sulfide when disturbed. Lauterborn (1901) designates this type of deposit as *sapropel,* being largely derived from cellulose-rich detritus of higher plants or *förna.* In addition, coprogenic sediments, produced by the

Fig. 3. — Dead Hat Pond, looking south.

action of the bottom fauna on settled planktogenic sediments (*ävja*), are present, which Naumann (1929) terms *gyttja*. Lindemann (1941) points out that sediments do not always appear as pure "genotypes," and that a certain amount of variation and intergradation must be expected. It should be noted that the bottom deposits of Dead Hat Pond are not as thick as those of Washboiler Pond, and that the sediments of the eastern half of Dead Hat Pond are intermixed with sand and pebbles.

Washboiler Pond and Dead Hat Pond are aestival ponds in that they contain some water throughout the open season, but freeze to the bottom during the winter months (Welch, 1952). Being in the alpine zone, they are characterized by short open seasons. The ice had completely disappeared by mid-July, but by late October both ponds had acquired an ice cover of sufficient thickness to support a person's weight.

MATERIALS AND METHODS

Visits were made to the site at intervals of 5 to 11 days from July 18, 1957 to October 19, 1957. All visits were made between 9:30 a.m. and 2:00 p.m. Since the route from the road to the site of the ponds was quite steep, the lightest and most compact equipment was essential.

The hydrographic maps (Figs. 4 and 5) are the result of a series of photographs and routine measurements, carried out as follows. A grid, 10 meters square, was constructed of string and stakes over each pond, and the outline of each pond was sketched on graph paper according to the appropriate scale. The depth contours were interpolated from a series of depth measurements made with a meter stick. A mapping compass was used to establish a north-south baseline.

Surface and bottom temperatures were recorded for both ponds during each visit. A standard laboratory thermometer was utilized for this purpose. When temperatures were found to be variable in different areas of the ponds, mean surface and bottom temperatures were calculated for each pond.

Four water samples were taken during the open season from each pond for purposes of color and pH determinations. Color determinations were carried out in the laboratory by means of the platinum-cobalt method (see Welch, 1948). For pH determinations, permanent Hellige discs were used in conjunction with the appropriate indicator solutions.

Nine water samples were taken from each pond during the open season for routine free carbon dioxide and bound carbon dioxide determinations in the laboratory. Free carbon dioxide was determined by sodium hydroxide titration, and bound carbon dioxide was determined by hydrochloric acid titration. Phenolphthalein and methyl orange indicators were utilized in the sodium hydroxide and hydrochloric acid titrations, respectively. Results were calculated in parts per million (ppm).

Two 3.9 liter water samples were taken from each pond near the beginning and near the close of the open season, for residue determinations. In each case, the entire sample was evaporated in a large evaporating dish placed in a sand bath. The residue which remained in the evaporating dish was ignited at 600° C, and the loss on ignition by weight was determined. The amounts of organic residue and inorganic salts present were calculated in terms of milligrams per liter.

Toward the close of the open season, a sediment sample was taken from each pond. An aliquot from each sample was dried and ignited at 600° C. The loss on ignition by weight was determined, and the percentages of organic matter and inorganic matter in the sediment were calculated in each case.

The bottom fauna was sampled by means of a scoop (12 x 12 x 2.8 cm) constructed of heavy sheet metal. Each sample consisted of one-seventieth of a square meter. Two samples were taken from each pond during each visit, one near the area of maximum depth and one in a relatively shallow area. The sample was strained through a number 20 wire screen sieve and placed in a small jar of 95 percent ethyl alcohol. The organisms were sorted, according to taxonomic categories, into smaller vials of 95 percent ethyl alcohol upon arrival at the laboratory.

For zooplankton a wide-mouthed 2.7 liter bottle was used. Two samples were taken from each pond during each visit, one near the

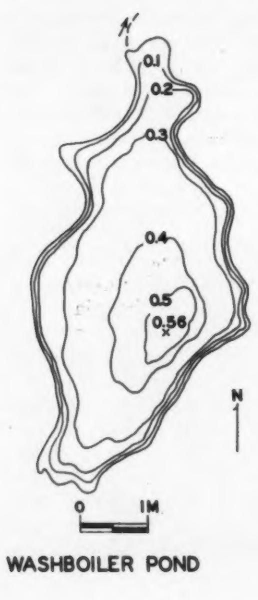

Fig. 4. — Hydrographic map of Washboiler Pond. Depths in meters.

surface and one near the bottom. The samples were strained through number 20 bolting silk, and the organisms were transferred to vials of 95 percent ethyl alcohol. In the laboratory, the entire liter sample was counted, using a 1 cc Sedgewick-Rafter counting chamber. The author feels that this method reduces the chances of overlooking zooplankters of rare occurrence. Reviews of some plankton sampling methods are presented by Kutkuhn (1958), Littleford *et al.* (1940), and Serfling (1949).

Since the visits to the ponds were somewhat irregular, running averages of three points were computed in the preparation of benthic fauna and zooplankton population data. It is thought that such a running average renders a better overall picture of the population trends.

Miscellaneous organisms, which were too few in numbers to be taken in the quantitative samples, were taken by means of random sweeps with an aquarium dipnet along the shorelines of the ponds. Specimens were transferred to vials of 95 percent ethyl alcohol, and were identified in the laboratory.

RESULTS

PHYSICAL CHARACTERISTICS

Temperature.—Surface and bottom temperatures are summarized in Table I. In general, the temperatures recorded for Dead Hat Pond were higher than those of Washboiler Pond, perhaps being partially due to the fact that Dead Hat Pond has a larger surface area per unit volume.

On October 12 and October 19 very thin melting ice films were noted on the surfaces of both ponds, which fact presumably explains the occurrence of lower surface than bottom temperatures on these

TABLE I.—Mid-day water temperatures (°C)

Date		Washboiler Pond		Dead Hat Pond	
		Surface	Bottom	Surface	Bottom
July	18	12.0	10.3	12.9	9.3
July	26	13.0	11.0	12.5	11.0
August	2	16.0	14.0	19.8	15.8
August	9	17.5	13.5	18.0	15.0
August	16	14.5	11.5	15.0	13.5
August	26	13.0	11.0	12.0	12.0
August	31	7.0	7.0	8.5	8.0
September	10	10.0	7.5	10.0	10.0
September	19	10.0	8.0	10.5	8.5
September	28	10.0	9.0	10.5	9.0
October	5	9.5	7.5	10.0	7.5
October	12	9.0	9.5	8.0	8.0
October	19	0.5	4.5	4.5	6.0

TABLE II.—Color determinations

Date	Washboiler Pond	Dead Hat Pond
August 9	100	60
September 10	100	70
October 12	100	60
October 19	60	50

dates. Apparently the morning sun had not yet warmed the surface waters.

Temporary "microthermoclines" between surface and bottom were common in both ponds throughout the open season. This phenomenon may be attributed, in part, to the facts that both ponds are well protected by hills on all sides and that their small size presents a relatively small surface area to the atmosphere, so that even during high winds their surfaces are unruffled. It is thought that these conditions prevent the mixing of surface and sub-surface waters. It may

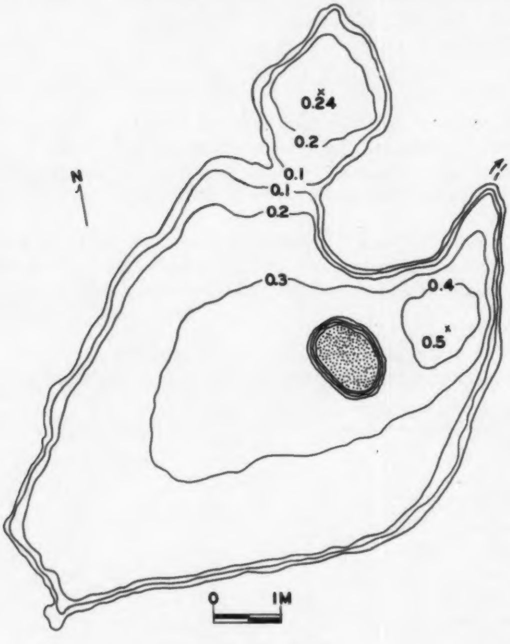

Fig. 5. — Hydrographic map of Dead Hat Pond. Depths in meters.

also be stated that, even under relatively warm weather conditions, when solar insolation is high, the ponds may maintain a warm upper layer, while the sub-surface waters remain relatively cold, due to the poor heat conduction by the water. This phenomenon is not peculiar to alpine ponds, but is common to ponds in general. Welch (1952) has found situations during the summer months in which within a depth of about 0.6 meters there was a difference of more than 6° C between bottom and surface temperatures.

Two European investigators, Pesta (1933) and Pichler (1939a, 1939b), have recorded daily variations of 7 to 20° C and 6.5 to 30° C, respectively, in alpine ponds. Presumably comparable variations occurred in Washboiler and Dead Hat Ponds.

Color.—Considering the humic contents of the bottom deposits in Washboiler Pond and Dead Hat Pond, it is not surprising that the water color was quite high in the ponds (Table II). The waters of both ponds possessed a weak tea color. Washboiler Pond maintained a value of 100 until the close of the open season when the color value dropped to 60. The values obtained for Dead Hat Pond were, in general, lower than those of Washboiler Pond, decreasing to a value of 50 by the end of the open season. Presumably the color values obtained were a function of the humic activity in bottom deposits and surrounding surface drainage. Dead Hat Pond possesses a thinner stratum of organic bottom material than does Washboiler Pond.

CHEMICAL CONDITIONS

Hydrogen-ion concentration.—The pH determinations covered a rather narrow range during the open season in both ponds, always being slightly acid. Washboiler Pond and Dead Hat Pond showed ranges of pH 6.0-6.4 and pH 6.0-6.8, respectively. These ranges are indicative of small amounts of dissolved solids, the presence of some free carbon dioxide, negligible photosynthesis, and the effects of weak organic acids of humic origin.

Carbon dioxide.—Free carbon dioxide determinations were, in general, low for both ponds. The highest seasonal reading obtained was 3 ppm in Washboiler Pond on August 9. Presumably this reading, as compared to relatively protected waters at lower altitudes, can be attributed in part to the low partial pressure of carbon dioxide at 3,582 meters elevation, and in part to the slow rate of metabolic release of carbon dioxide into the water.

Bound carbon dioxide determinations averaged 3.2 ppm in Washboiler Pond, and 3.7 ppm in Dead Hat Pond. The highest seasonal reading of 9 ppm was recorded in Washboiler Pond on October 5. Pennak (1958) points out that this situation is presumably a reflection of the youth of alpine waters, since such waters result from rains and snows and are in contact with the substratum for only a short time.

According to Pennak (1945) the alpine zone is characterized by

"soft" waters. This situation is not surprising, considering that the rocks and soils in the northern Colorado mountain area are low in carbonate content. Data presented by Ström (1928), however, indicate that the rocks and soils of certain European mountain districts are rich in carbonates.

Dissolved salts.—Total ash content ranged from 23.1 mg per liter to 27.8 mg per liter in Washboiler Pond, and from 18.2 mg per liter to 19.9 mg per liter in Dead Hat Pond, in keeping with the data presented by Neldner and Pennak (1955). Pennak (1958) points out that this relatively low total ash content is an additional reflection of the "newness" of alpine waters, being due to the fact that the rocks of the alpine zone in Colorado are relatively insoluble.

Total organic matter.—Unfortunately, the literature, including loss on ignition data for ponds in general, is meager. Neldner and Pennak (1955) record a range of 17.5 to 38.4 mg per liter in Trail Ridge Pond, Rocky Mountain National Park, Colorado. Total organic matter in Washboiler and Dead Hat Pond ranged from 11.1 to 19.3 mg per liter and from 9.5 to 9.9 mg per liter, respectively. The amount of dissolved organic matter depends on such factors as the biota, geological history of the area, nature of the bottom deposits, drainage, precipitation, wind-blown material, and physico-chemical conditions of all kinds.

Substrate.—Previous reference has been made to the nature of the bottom deposits of both ponds. Substrate analysis for Washboiler Pond revealed that the bottom deposits contained 52.1 percent organic matter, and the bottom deposits of Dead Hat Pond contained 51.6 percent. Comparable data for other alpine ponds are almost lacking. When sufficient information becomes available, the possibility of classifying sediments can be explored further.

BIOLOGICAL CHARACTERISTICS

Vegetation.—Since many tundra ponds are temporary and dry up during some part of their open season, they support no aquatic vegetation (Neldner and Pennak, 1955). However, both Washboiler Pond and Dead Hat Pond are permanent bodies of water and support emergent growths of *Carex aquatilus* Wahl. at depths of 0.1 m and less; neither pond supports rooted aquatic vegetation at greater depths (compare Figs. 2 and 3 with Figs. 4 and 5). This condition is to be expected since (1) *Carex* apparently does not grow at depths exceeding 0.1 m under the prevailing ecological circumstances, and (2) neither pond has sufficient depth or other ecological conditions to permit the development of aquatic plant zonation.

Apparently the limited growth of *Carex* provides extra ecological niches for metazoans present in the ponds. The greatest variety of metazoans was taken at depths of 0.1 m or less.

Bottom Fauna.—Sampling revealed that the benthic fauna was qualitatively scanty, and that three groups of organisms were domi-

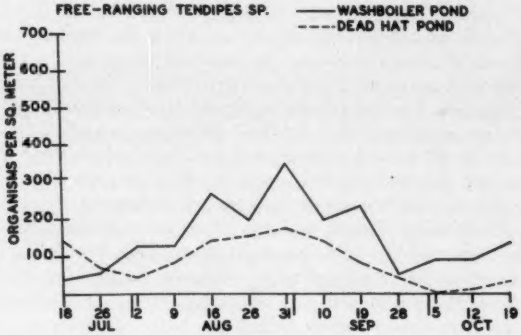

Fig. 6. — Open season population curves for free-ranging *Tendipes* sp. in the bottom deposits during 1957.

nant in both ponds: Diptera (Tendipedidae), Pelecypoda (Sphaeriidae), and Oligochaeta (Tubificidae). Certain other groups of bottom-dwelling organisms, which were quantitatively scanty, occurred in both ponds; these will be discussed in a later section.

Only one species of the dipteran, *Tendipes* sp., was present in the superficial bottom deposits of the two ponds throughout the entire open season. All individuals were in the form of free-ranging larvae during the first half of the open season, and the great majority of larvae were in cocoons during the second half of the open season. Free-ranging *Tendipes* were present by the time the ice had disappeared in mid-July (Fig. 6). On July 18, 35 and 140 individuals per square meter were present in Washboiler Pond and Dead Hat Pond, respectively. On August 31, a seasonal maximum of 350 free-ranging

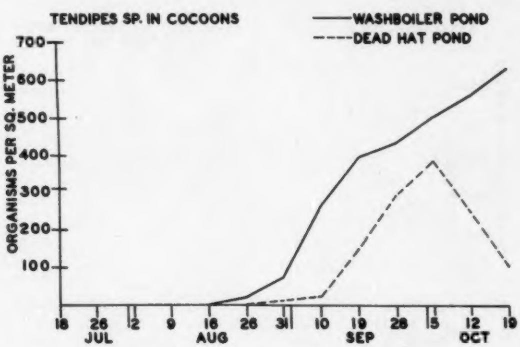

Fig. 7. — Open season population curves for *Tendipes* sp. in cocoons in the bottom deposits during 1957.

larvae per square meter was reached in Washboiler Pond and 175 in Dead Hat Pond. After this date, a relative decrease in free-ranging *Tendipes* populations was noted toward the close of the open season.

As early as August 16 *Tendipes* in cocoons appeared in the bottom samples (Fig. 7). These cocoons were oblong in shape, round in cross-section, and constructed of a silk-like substance secreted by the larva. Numbers of cocoon forms increased as the free-ranging larvae decreased toward the end of the open season (compare Fig. 6 with Fig. 7); a maximum of 630 cocoons per square meter was found on October 19 in Washboiler Pond, while a seasonal maximum of 388 individuals was attained on October 5 in Dead Hat Pond. It is possible that the decrease in numbers of cocoons in Dead Hat Pond during October may be attributed to sampling error. Presumably, then, *Tendipes* overwinters in cocoons, and the early appearance of cocoons is in anticipation of the early winter conditions common in the alpine tundra. Since cocoons were not recovered at the beginning of the open season, it seems likely that with the advent of the spring thaw, the larvae immediately pupate and emerge as adults. The adults deposit their eggs, which hatch early in the open season, and the small free-ranging larvae taken in July are early instars hatched from eggs deposited during the same early summer. It is interesting to note that the larvae found in the cocoons later in the season were larger, indicating perhaps that the capacity to produce such hibernacula is limited to the later instars. Judging from the unimodal population curve exhibited by both free-ranging larvae and cocoon forms, it seems that later instars of *Tendipes* overwinter, and produce one generation of adults each year, early in the open season (Figs. 6 and 7).

In contrast to *Tendipes,* the dipteran, *Metriocnemus* sp., presented a bimodal population curve, being most abundant at the beginning and at the end of the open season (Fig. 8). The two population peaks

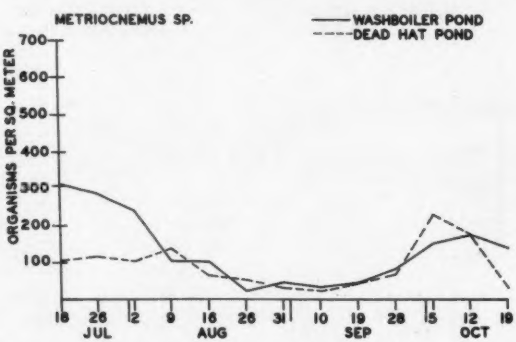

Fig. 8. — Open season population curves for *Metriocnemus* sp. in the bottom deposits during 1957.

found for each pond were 315 and 175 individuals per square meter on July 18 and October 12, respectively, in Washboiler Pond, and 140 and 232 on August 9 and October 5, respectively, in Dead Hat Pond. A seasonal minimum of 23 individuals per square meter was recorded in Washboiler Pond on August 26 and in Dead Hat Pond on September 10. The small numbers of individuals during August and September coincided with the greatest abundance of *Tendipes*. Apparently, then, *Tendipes* "replaces" *Metriocnemus* during the midseason. This situation is possibly an example whereby two species, separated by generic characters, exist at different times within the same area, while presumably drawing upon a common pool of resources (Elton, 1946). The population data for *Metriocnemus* would indicate that two generations are produced each year, one very early in the open season and one during midseason. Since no cocoon forms were observed, the later instar larvae taken near the close of the open season apparently overwinter in the deeper mud layers, immediately pupating and emerging as adults as soon as the ice melts in the spring. The smaller larvae taken during July were undoubtedly early instars hatched from eggs deposited earlier during the open season. Later instars were noted early in August; the notable decrease in numbers of these late instars during August and September are associated with a second emergence of adults.

Population densities of small oligochaetes of the Family Tubificidae were irregular during the entire open season (Fig. 9). Numbers of individuals per square meter ranged from 70 to 490 in Washboiler Pond and from 0 to 35 in Dead Hat Pond. As might be expected, the thicker organic deposits in the bottom sediments of Washboiler Pond supported a larger population of Tubificidae. In other words, the thinner organic deposits intermixed with sand and gravel in Dead Hat Pond may be an important limiting factor, which accounts for the almost negligible population of tubificid oligochaetes.

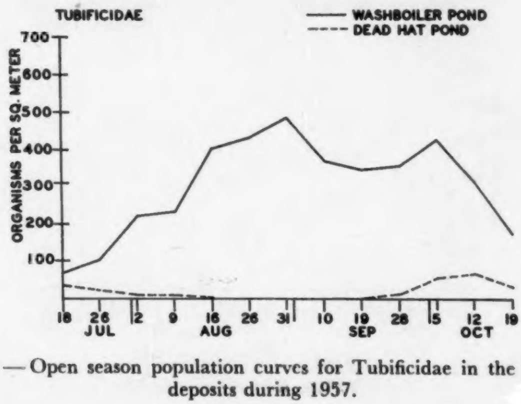

Fig. 9. — Open season population curves for Tubificidae in the bottom deposits during 1957.

Quantitatively, the bivalve mollusk *Pisidium casertanum* Poli was least abundant among the organisms taken in the bottom samples (Fig. 10). It should be noted, however, that *Pisidium* was relatively more abundant throughout the open season in Dead Hat Pond, attaining a seasonal maximum of 163 individuals per square meter on July 26, while a seasonal maximum of 140 individuals was recorded in Washboiler Pond on July 18. This situation is in direct contrast to that represented by the Tendipedidae and Tubificidae, which were relatively more abundant in Washboiler Pond. Perhaps the occurrence of a small amount of sand and gravel mixed in the bottom sediments of Dead Hat Pond partially explains the greater numbers of *Pisidium*. According to Pennak (1953), stable sand, gravel, and substrates composed of sand or gravel mixed with other materials support the largest bivalve populations. Very little is known about *Pisidium* biology, but apparently the adults are able to overwinter by migrating to the deeper layers of the substrate when the ponds freeze to the bottom, and returning to the more superficial layers at the time of the spring thaw.

Population densities of individual species were quite high, but only a few species were present. Numerical differences in the populations of the two ponds were not greatly significant, except for the Tubificidae. Table III, however, presents a summary of the mean open season standing crop of benthic fauna, calculated in terms of pounds per acre wet weight, which can be compared with representative published data for certain lakes. Townes (1938) found that Chautauqua Lake, in New York State, is unusually rich in benthic fauna with an average of 390 kilograms per hectare (374 pounds per acre). Townes further considers a natural lake, yielding 300 kilograms per hectare (267 pounds per acre) of bottom fauna, to be "normally rich." Sublette (1957) found that the total mean annual standing crop of

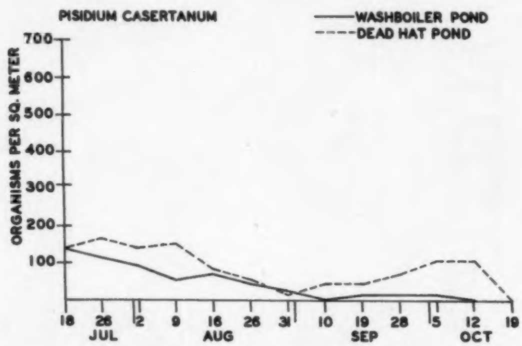

Fig. 10.—Open season population curves for *Pisidium casertanum* Poli in the bottom deposits during 1957.

benthic fauna in Lake Texoma, Oklahoma and Texas, was 125 kilograms per hectare (111 pounds per acre), which is rather poor by comparison with Townes' data. If compared with Townes' standard, an average of 286 pounds per acre for both Washboiler and Dead Hat Ponds are at least "normally rich," in spite of the small size of the ponds and the prevailing severe ecological conditions of the alpine tundra. (For further comparison with other lakes, see Deevey, 1941 and Rawson, 1953.) Until further studies can be conducted, it is to be hoped that this summary of the mean open-seasonal standing crop for Washboiler and Dead Hat Ponds will serve as an index to the benthic productivity of small alpine tundra ponds.

TABLE III. — Mean open season standing crop (bottom fauna) in pounds per acre wet weight

	Washboiler Pond	Dead Hat Pond
Free-ranging *Tendipes* sp.	69	38
Tendipes sp. in cocoons	109	45
Metriocnemus sp.	58	42
Pisidium casertanum	27	51
Tubificidae	125	8
Total	388	184

Zooplankton.—The zooplankton populations in Washboiler Pond were quantitatively high, but qualitatively scanty; populations in Dead Hat Pond, on the other hand, were both quantitatively and qualitative-

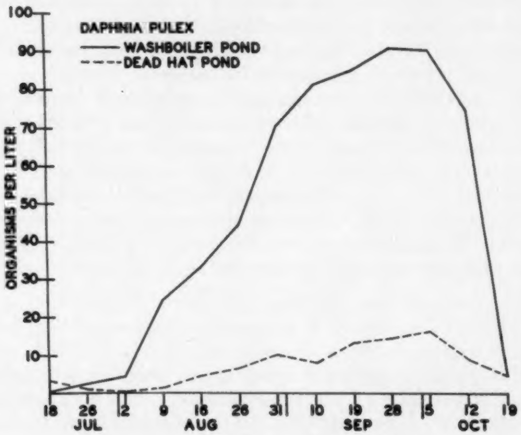

Fig. 11. — Open season population curves for *Daphnia pulex* DeGeer in the plankton during 1957.

ly poor (for a comparison with alpine lakes see Pennak, 1955 and Rawson, 1942, 1956). Four major groups of zooplankters were represented: Cladocera (*Daphnia pulex* DeGeer and *Chydorus sphaericus* Baird), Copepoda (*Canthocamptus sinuus* Coker and *Cyclops varicans* Sars), Rotatoria (*Keratella cochlearis* Gosse), and Protozoa (*Actinophrys sol* Ehrenberg).

Daphnia pulex was the dominant zooplankter in both ponds (Fig. 11). However, a striking difference in numbers of individuals of this species was noted between the two ponds. The population curve was unimodal in Washboiler Pond. A seasonal maximum of 91 individuals per liter was recorded on September 28. In Dead Hat Pond a definite population pattern was difficult to discern, and a seasonal maximum of only 16 individuals was attained on October 5. Although this situation is in keeping with the generally lower benthic productivity of Dead Hat Pond, the vast difference in zooplankton counts is difficult to explain unless the source and availability of food are considered the major limiting factors. Pennak (1957) refers to a "food niche" or a "functional niche" in which animals are commonly relegated to a niche on the basis of their food habits, with little regard to their other requirements. The "habitat niche" concept, however, is not to be forgotten, whereby the entire water mass imposes a continuum of ecological factors upon all the fauna present. The results of this study would indicate that, with the exception of the source and availability of food, a common set of limiting factors, physical and organic, are acting in combination upon the animal communities in both ponds.

It is not surprising to find *Daphnia pulex* in small permanent alpine ponds, for this species is widely distributed and common everywhere, except in rapidly flowing streams and grossly polluted waters. Its widespread distribution is presumably due to the production of resistant ephippial eggs, which can be transported widely by various agents. Since ephippia are an adaptation to adverse conditions, fertilized females in a population will produce ephippial eggs in anticipation of the winter months, especially in shallow bodies of water where the entire water mass may freeze to the bottom or to such an extent that winter anaerobiosis is prevalent. Ephippia appeared well in advance of the early winter freeze, which usually occurs in middle to late October on the alpine tundra. True ephippia were recovered as early as August 16 in Washboiler Pond and August 26 in Dead Hat Pond, increasing in numbers toward the end of the open season.

Another cosmopolitan cladoceran species, *Chydorus sphaericus*, occurred regularly, attaining a seasonal maximum of 9.8 individuals per liter in Washboiler Pond as compared with only 0.7 in Dead Hat Pond. Although not supported by other investigations, Smyly (1957) refers to *C. sphaericus* as a "weed species," being common among aquatic vegetation. Since all quantitative zooplankton sampling was conducted in open water, it might be expected that larger numbers of *C. sphaericus* could be found among the *Carex* growths. Qualitative

sampling in the emergent vegetation along the shoreline, however, only revealed an occasional specimen.

Among the Copepoda, isolated specimens of the bottom-feeding harpacticoid *Canthocamptus sinuus* and the cyclopoid *Cyclops varicans* were taken regularly from both ponds. Distribution records for the United States indicate that *Canthocamptus sinuus* has been reported only from Connecticut, New York, and North Carolina. *Cyclops varicans* is a small variable species, reported mostly from Europe and Asia. A few records have been given for the eastern half of the United States. *C. varicans* is an inhabitant of ponds and the vegetated zone of lakes. It appears, then, that *Canthocamptus sinuus* and *Cyclops varicans* are essentially new records for the Colorado mountain area.

The altitudinal, as well as the geographic, distribution of Copepoda is difficult to explain. The Harpacticoida produce non-resistant resting eggs, and any explanation other than active migration via a single drainage system seems remote. It is interesting to note, however, that the Cyclopoida produce resistant copepodid cysts, which would make possible passive dispersal by various agents (Pennak, 1953).

Rotatoria and Protozoa populations were negligible. A single specimen of *Keratella cochlearis* was recorded from Washboiler Pond on July 18. That Rotatoria were almost non-existent is especially surprising, since this situation leaves an entire ecological niche vacant. Two specimens of the "sun animalcule," *Actinophrys sol*, were observed in the zooplankton samples from Dead Hat Pond, one on July 18 and one on August 2.

Phytoplankton.—Generic determinations were made on the phytoplankton contained in the zooplankton samples. Since the number 20 silk bolting cloth used in zooplankton sampling was too coarse to retain all phytoplankters, quantitative determinations were not made. Casual observations revealed that the population was quantitatively scanty, but that a considerable variety of genera was represented. The following list of genera is not intended to be complete, but it contains the majority of phytoplankton genera present in the ponds.

Chrysophyta	Chlorophyta	Cyanophyta
Asterionella	*Ankistrodesmus*	*Gloeocapsa*
Cymbella	*Closterium*	*Nostoc*
Fragilaria	*Cosmarium*	*Polycystis*
Melosira	*Dinobryon*	
Navicula	*Micrasterias*	
Pinnularia	*Microspora*	
Stephanodiscus	*Spirogyra*	
Tabellaria	*Staurastrum*	
	Zygnema	

Early in August small greenish, spherical objects resembling *Nostoc* "marbles" were observed floating on the surfaces and clinging to the

emergent sedges around the peripheries of both ponds. Neldner and Pennak (1955) observed such peculiar balls in Trail Ridge Pond, Larimer County, Colorado, and described them as colonies of an unknown ciliate containing symbiotic (?) algal cells, associated with numerous desmids and diatoms; the entire mass was held together by a gelatinous matrix. Dissection and microscopic examination, however, revealed that the objects found in Washboiler and Dead Hat Ponds were colonies of *Polycystis* (=*Microcystis*) *incerta* Lemm., consisting of closely packed, pseudovacuolated cells embedded in a gelatinous matrix. Other blue-green algae, filamentous green algae, desmids, diatoms, and an occasional *Daphnia pulex* were often found associated with these colonies. Whether these associated organisms were deriving some benefit from the colonies, or were simply trapped in the gelatinous mass, the author is at a loss to state. These colonies increased in numbers, and by the end of the summer they formed continuous greenish rings around the peripheries of both ponds. Smith (1950) associates *Polycystis* "water blooms" with hard-water lakes, but the chemical determinations conducted in this study would indicate that hardness or softness of the water is not necessarily a primary limiting factor.

It is interesting to note that most of the diatom cells observed in the zooplankton samples were dead. However, the great majority of blue-green algae, filamentous green algae and desmids were live cells.

Miscellaneous organisms.—During the open season several species of metazoans were taken in the qualitative samples along the shoreline and were not found in the quantitative bottom samples. The groups which were represented are as follows: Trichoptera (*Limnephilus* sp.), Hemiptera (*Notonecta undulata* Say), Diptera (*Aedes* sp.), Coleoptera (*Agabus* sp. and *Hygrotus* sp.), Hydracarina (*Limnesia* sp.) and Rhabdocoela (*Mesostoma* sp.).

Although numerous *Limnephilus* cases appeared in the quantitative bottom samples (apparently accumulated from populations of previous years), cases containing living larvae were very few in number. It is interesting to note that the majority of caddisfly larvae taken in Washboiler Pond constructed their cases of bits of vegetable matter, while most larvae in Dead Hat Pond constructed their cases of fine sand grains. This phenomenon would indicate that these animals take the best advantage of the ecological opportunities offered in adapting themselves to a given environment.

Notonecta undulata was the only aquatic hemipteran taken in both ponds. This species was present in the shallows among the emergent vegetation throughout the field season, but individuals were always few in number.

Aedes (Culicidae) larvae were abundant near the shoreline of the two ponds during late July. By early August the larvae had pupated and emerged as adults. It was during early August that field work was most unpleasant for the author, due to a super-abundance of adult mosquitoes.

Agabus (Dytiscidae) was the only beetle taken from both Washboiler Pond and Dead Hat Pond throughout the open season. This genus was always found in association with the emergent *Carex* growths. A single specimen of *Hygrotus* was taken from Washboiler Pond on September 28.

On September 10 and October 12, small populations of the rhabdocoel *Mesostoma* (Typhloplanidae) were observed on the mud surface along the southeast shore of Dead Hat Pond. It was on these same dates that a maximum depth of approximately 0.3 meters was recorded in both ponds, and the waters were especially stagnant. Present knowledge indicates that non-triclad turbellarians are associated with stagnant bodies of water (Pennak 1953). No turbellarians were found in Washboiler Pond. In all individuals examined the uteri were found to be distended with thick-shelled "winter" eggs, presumably an adaptation to adverse environmental conditions.

Hydracarina were taken in Washboiler Pond only during August. Individuals were never abundant, and *Limnesia* was the only representative found.

During August one specimen each of a fresh-water nematode and an ostracod (Podocopa) were recovered from the bottom samples of Washboiler Pond. Owing to the difficult systematics of these two groups and the lack of sufficient material, a taxonomic determination was not made.

DISCUSSION

Alpine pond situations, as represented by the Washboiler and Dead Hat Pond types, apparently have not been described in the American limnological literature except by Neldner and Pennak (1955) who described an alpine pond (Trail Ridge Pond) in Rocky Mountain National Park, Colorado. The same general taxonomic groups were represented in Trail Ridge Pond that were found in Washboiler Pond and Dead Hat Pond. Since Trail Ridge Pond is considerably larger and contains more emergent vegetation than either of the two ponds considered in the present study, a greater number of ecological niches were available to organisms adapted to the alpine aquatic environment, and consequently more species were represented within these taxonomic groups. It is notable, in addition, that Trail Ridge Pond had an abundance of phyllopod crustaceans, while this group was never collected in Washboiler and Dead Hat Ponds.

Blake (1945) has briefly characterized some small moraine ponds at an elevation of 10,200 feet in the Medicine Bow Mountains of Wyoming. These ponds apparently have a morphometry very similar to that of Washboiler Pond and Dead Hat Pond. However, owing to the less rigorous climatic conditions afforded by the forested montane zone, these moraine ponds are characterized by a longer open season and higher water temperatures. Such conditions would offer a more desirable habitat for a greater variety of animal species such as dragon-

fly and damselfly nymphs, and a variety of beetles, leeches, and amphibians.

McClure (1943) has described some temporary and permanent alpine tundra ponds in the Churchill, Manitoba, Hudson Bay area. The latter are comparable to Washboiler and Dead Hat Ponds. However, these ponds differed qualitatively and quantitatively with regard to faunal characteristics; Pelecypoda were entirely absent, and snails, leeches, hydras, and odonate nymphs were found to be present. Also, one of these ponds had a seasonal maximum of 80,000 metazoans per cubic foot of water, which is not short of a eutrophic situation. McClure's physical and chemical data are not adequate for comparison, but it would appear that these Canadian alpine tundra ponds are characterized by a longer open season and higher water temperatures, and are not subjected to the rigorous climatic conditions of the alpine tundra of the Colorado Rockies.

Numerous "Almtümpeln" and "Teichen" have been characterized by many European investigators. These ponds resemble Washboiler and Dead Hat Ponds in certain respects, but richer quantitative and qualitative phyto- and zooplankton populations have invariably been reported.

Seasonal variations are extreme. In general both Colorado ponds had a qualitatively impoverished fauna. Low summer temperatures and the climatic conditions which affect temperature, are apparently important limiting factors during the open season. It appears that, owing to the extremely small size of these two ponds, the aquatic environment is subject to great variation, and the temperatures to which aquatic organisms are subjected are as much a function of pond size as of altitude. It is not clear as to what other ecological factors, such as source and availability of food, are of importance as primary limiting factors. It may be said, however, that, due to the relative "newness" of alpine waters, the waters of Washboiler Pond and Dead Hat Pond are characterized by low dissolved materials and organic content acting in combination with physiographic and climatic factors to produce a poor fauna. It also seems that the extended winter freeze and short open season would necessitate a permanent fauna, which (1) can burrow deeply into the mud and endure long periods of winter anaerobiosis, or (2) can endure for long periods in the form of resistant eggs or cysts.

Certain major taxonomic groups commonly represented in ponds at lower altitudes were not taken from Washboiler and Dead Hat Ponds. These include phyllopods, amphipods, mayfly nymphs, odonate nymphs, and snails. That phyllopods are not temporary inhabitants of Washboiler and Dead Hat Ponds cannot be stated with any degree of certainty, since these animals may be absent for a year or two and then reappear for one, two, three, or more consecutive years (Neldner and Pennak, 1955).

Small permanent and temporary ponds occur commonly on the alpine tundra of the Colorado mountain area wherever the availability

of sufficient drainage from melting snows and summer showers exists. Permanent alpine pond types vary considerably in size, shape, and depth, and are not comparable to the temporary alpine type. The permanent alpine pond type is more like the temporary pond type found at lower altitudes, where long periods of drought replace the extended winter freeze and where organisms are obliged to endure long resting phases of very low activity with little ill effect or else to perish (Livingstone *et al.,* 1958).

All genera and some species found in Washboiler and Dead Hat Ponds occur in ponds at lower altitudes and are not restricted to an alpine aquatic environment. Casual observations made on several other small permanent alpine tundra ponds during the open season of 1957 showed that the *Pisidium* - tendipedid - *Daphnia* association is not uncommon.

Since small permanent ponds are common on the alpine tundra, their role in alpine ecology is not negligible. Because the scanty biota is dormant for nearly 9 months of the year, the ultimate succession of such ponds is relatively slow, and processes such as the decay of dead organic matter and the coprogenic activities of the biota contribute only slowly to the organic content of the bottom sediments and subsequent soil formation.

SUMMARY

Washboiler Pond and Dead Hat Pond are two small alpine tundra ponds located on the western slope of the Continental Divide in Summit County, Colorado, at an elevation of 3,582 meters (11,750 feet). Washboiler Pond is 2 by 6 meters and 0.56 m deep, and Dead Hat Pond is 4 by 9 meters with a maximum depth of 0.5 m.

This study extended from July 18 to October 19, 1957, and this period represented the entire open season for that year. Visits were made at 5 to 11 day intervals.

Routine physical and chemical determinations were conducted. It was found that both ponds are characterized by low temperatures, highly colored water, slightly acid pH, and low dissolved solids and organic content.

Emergent growths of *Carex aquatilus* were the only rooted aquatic plants present in either pond.

Quantitative and qualitative sampling was carried out in connection with the bottom fauna and zooplankton. Quantitative determinations revealed that *Tendipes, Metriocnemus,* and *Pisidium casertanum* were the dominant bottom organisms common in both ponds. Free-ranging *Tendipes* reached a seasonal maximum of 350 individuals per square meter in Washboiler Pond on August 31, tapering off thereafter and being replaced by an increasing number of *Tendipes* in cocoons toward the close of the open season. Both free-ranging and cocoon forms represented the same species of *Tendipes. Metriocnemus* had a bimodal population curve, with distinct peaks during July and September in both ponds. *Tendipes* produced one generation per

year, while *Metriocnemus* produced two generations per year.

Tubificidae were almost negligible in Dead Hat Pond, but populations varied from 70 to 490 individuals per square meter in Washboiler Pond.

Pisidium casertanum was most abundant in Dead Hat Pond, attaining a seasonal maximum of 163 individuals per square meter on July 26. On the whole, *Pisidium* was the least abundant of all bottom organisms taken during the open season.

Total mean open season standing crops were 388 pounds per acre wet weight in Washboiler Pond and 184 pounds per acre wet weight in Dead Hat Pond. The benthic productivities of both ponds are compared with those of certain North American lakes.

Daphnia pulex was the dominant zooplankter in both ponds, reaching a seasonal maximum of 91 individuals per liter in Washboiler Pond on September 28, and only 16 individuals in Dead Hat Pond on October 5. Ephippial eggs were recovered as early as August 16 in Washboiler Pond. *Chydorus sphaericus* and the copepods, *Canthocamptus sinuus,* and *Cyclops varicans,* occurred in the two ponds as incidental zooplankters.

Rotatoria and Protozoa were very rare. A single specimen of *Keratella cochlearis* and two specimens of *Actinophrys sol* were taken from Washboiler and Dead Hat Ponds, respectively, during the entire open season.

Quantitative determinations were not made on the phytoplankton, but representatives of the Chrysophyta, Chlorophyta, and Cyanophyta were observed in the zooplankton samples.

The following animals were taken in the qualitative samples near the shoreline: *Limnephilus* (Trichoptera), *Notonecta undulata* (Hemiptera), *Aedes* (Diptera), *Agabus* and *Hygrotus* (Coleoptera), *Mesostoma* (Rhabdocoela), and *Limnesia* (Hydracarina). A single specimen of a nematode and an ostracod (Podocopa) were recovered from the bottom sample.

Washboiler Pond and Dead Hat Pond are compared with other small alpine, arctic, and sub-arctic ponds in North America and Europe, and with temporary ponds at low altitudes.

In general, both ponds were poor in species. It is thought that low dissolved solids and low organic content acting in combination with physiographic and climatic factors are limiting factors.

Certain major groups common in ponds were not present in either pond; these include phyllopods, mayfly nymphs, odonate nymphs, and snails.

The most conspicuous single biotic aspect of the two ponds is the *Pisidium* – tendipedid – *Daphnia* community.

REFERENCES

BLAKE, I. H. 1945—An ecological reconnaissance in the Medicine Bow Mountains. Ecol. Monogr. **15**: 207-242.

BRINK, P. AND K. G. WINGSTRAND 1949—The mountain fauna of the Virihaure area in Swedish Lapland. Kungl. Fysiogr. Sällsk. Handl. N. F. **60**: 1-60.

DEEVEY, E. S. 1941—Limnological studies in Connecticut. VI. The quantity and composition of the bottom fauna of thirty-six Connecticut and New York Lakes. Ecol. Monogr. **11**: 413-455.

ELTON, C. 1946—Competition and the structure of ecological communities. Jour. Anim. Ecol. **15**: 54-68.

IVES, R. L. 1941—Tundra ponds. Jour. Geomorph. **4** : 285-296.

KUTKUHN, J. H. 1958—Notes on the precision of numerical and volumetric plankton estimates from small-sample concentrates. Limnol. and Oceanogr. **3**: 69-83.

LAUTERBORN, R. 1901—Die sapropelische Lebewelt. Zool. Anz. **24**: 50-55.

LINDEMANN, R. L. 1941 — The developmental history of Cedar Creek Bog, Minn. Amer. Midl. Nat. **25**: 101-112.

LITTLEFORD, R. A., C. L. NEWCOMBE, AND B. B. SHEPHERD 1940 — An experimental study of certain quantitative plankton methods. Ecology **21**: 309-322.

LIVINGSTONE, D. A., KIRK BRYAN, JR. AND R. G. LEAHY 1958—Effects of an arctic environment on the origin and development of fresh-water lakes. Limnol. and Oceanogr. **3**: 192-214.

MCCLURE, H. E. 1943—Aspection in the biotic communities of the Churchill area, Manitoba. Ecol. Monogr. **13**: 1-36.

NAUMANN, E. 1929—Einführung in die Bodenkunde der Seen. Die Binnengewässer **9**: 1-216.

NELDNER, K. H., AND R. W. PENNAK 1955—Seasonal faunal variations in a Colorado alpine pond. Amer. Midl. Nat. **53**: 419-430.

PENNAK, R. W. 1941—An introduction to the limnology of northern Colorado. Univ. Colo. Studies, Series D, **1**: 203-220.

———1945—Some aspects of the regional limnology of northern Colorado. Univ. Colo. Studies, Series D, **2**: 263-293.

———1953—*Freshwater invertebrates of the United States.* New York: Ronald Press Co. 769 pp.

———1955—Comparative limnology of eight Colorado mountain lakes. Univ. Colo. Studies, Ser. Biol. **2**: 1-75.

———1957—Species composition of limnetic zooplankton communities. Limnol. and Oceanogr. **2**: 222-232.

———1958—Regional lake typology in northern Colorado, U.S.A. Verh. internat. Ver. Limnol. **13**: 264-283.

PESTA, O. 1933—Beiträge zur Kenntnis der limnologischen Beschaffenheit ostalpiner Tümpelgewässer. Arch. Hydrobiol. **25**: 68-80.

———1935—Kleingewässerstudien in den Ostalpen. Arch. Hydrobiol. **29**: 296-345.

———1943—Limnologische Untersuchungen an einem Hochgebirgstümpel der Ostmark. Arch. Hydrobiol. **40**: 444-458.

———1948—Naturkundliches über Gebirgstümpel der Ostalpen. Natur und Land **9**: 234-243.

PICHLER, W. 1939a — Der Alpentümpel als Lebensstätte. Eine ökologische Studie. Bioklimatische Beibl. **6**: 85-89.

———1939b—Ergebnisse einer limnologischen Sammelfahrt in den Ostalpen. Arch. Hydrobiol. **35**: 107-160.

RAWSON, D. S. 1942—A comparison of some large alpine lakes in Western Canada. Ecology **23**: 143-161.

———1953—The bottom fauna of Great Slave Lake. Jour. Fish. Res. Bd. Canada **10**: 486-520.

———1956—The net plankton of Great Slave Lake. Jour. Fish. Res. Bd. Canada **13**: 53-127.

SERFLING, R. E. 1949—Quantitative estimation of plankton from small samples of Sedgewick-Rafter cell counts of concentrated samples. Trans. Amer. Micros. Soc. **68**: 185-199.

SMITH, G. M. 1950—*Fresh-water algae of the United States.* 2nd ed. New York: McGraw-Hill. 719 pp.

SMYLY, W. J. P. 1957—Distribution and seasonal abundance of Entomostraca in moorland ponds near Windermere. Hydrobiologia **11**: 59-72.

STIRNIMANN, F. 1926—Faunistisch-biologische Studien an den Seen und Tümpeln des Grimselüberganges. Internat. Rev. d. Ges. Hydrobiol. u. Hydrogr. **16**: 223-271.

STRÖM, K. M. 1928—Recent advances in limnology. Proc. Linn. Soc. London **140**: 96-100.

SUBLETTE, J. E. 1957—The ecology of the macroscopic bottom fauna in Lake Texoma (Denison Reservoir), Oklahoma and Texas. Amer. Midl. Nat. **57**: 371-402.

THOMASSON, K. 1951—Beiträge zur Kenntnis des Planktons einiger Seen in nordschwedischen Hochgebirge. Schweiz. Zeitschr. Hydrol. **13**: 336-351.

———1952—Beiträge zur Kenntnis des Planktons einiger Seen in nordschwedischen Hochgebirge. II. Schweiz. Zeitschr. Hydrol. **14**: 257-288.

TOWNES, H. K. 1938—Studies on the food organisms of fish. A biological survey of the Allegheny and Chemung watershed. VI. Suppl. to 27th Ann. Rept., 1937. State of New York Cons. Dept. Biol. Surv. (1937) **12**: 162-173.

TURNOWSKY, F. 1946—Die Seen der Schobergruppe in den Hohen Tauern. Carinthia II **8**: 7-78.

WELCH, P. S. 1948—*Limnological methods.* New York: McGraw-Hill. 381 pp.

———1952—*Limnology.* 2nd ed. New York: McGraw-Hill. 538 pp.

A Study of the Dynamics of a Population of Peromyscus gossypinus and P. nuttalli Subjected to the Effects of X-Irradiation

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A large number of experiments have been conducted in recent years that have demonstrated the deleterious effects of ionizing radiation in both individuals and in populations. It is a well established fact that if radiation is delivered to the gonads, inheritable changes will occur in the germ cells. The net effect of these changes is to increase the genetic variability of a Mendelian population, if the irradiated individuals are allowed to breed with other individuals in the population. The present paper is a report of the effects of x-irradiation on a natural population of two species of wild mice; the cotton mouse (*Peromyscus gossypinus*) and the golden mouse (*Peromyscus nuttalli*).

Studies on the dynamics of any natural population are important because the individuals that make up such a population are the basic units by which gene exchange is effected (Blair, 1953). It is generally recognized and accepted that any population of sexually reproducing organisms represents a gene pool from which the various combinations of genes that are best suited to a particular environment are chosen through the process of natural selection.

The present study was designed to analyze the effects of a presumed increase in genetic variation in mouse populations which were already well adapted to the environment in which they were living. It was expected that, in this case, the effects of x-irradiation would be revealed by a study of the dynamics of the two species populations as well as in the customary more easily measured morphological form.

This work was made possible by a grant from the U. S. Atomic Energy Commission (Contract No. AT (40-1)-1980). W. V. Robertson, Roger Williams, W. A. Stoddard, Norman Beal, Robert Timbrook and Roy Spradley served at various times as field assistants. The statistical calculations were made by Paul T. Koshi and Roy Spradley. George K. Stephenson, Officer-in-Charge, and the staff of the Southern Forest Experiment Station, U. S. Forest Service, were helpful with many phases of the study and deserve special thanks. Phil D. Goodrum helped with the field work. W. Frank Blair kindly read and criticised the manuscript.

Description of Study Area

The data to be presented later were derived from study plots located on the floodplain of the Angelina River in southwestern Nacogdoches County, Texas. The ecological community in which

these plots were located was described by McCarley (1954a) as a lowland or floodplain forest habitat. This habitat was normally heavily wooded and was characterized by the presence of stands of water oak (*Quercus nigra*), willow oak (*Q. phellos*), sweet gum (*Liquidambar styraciflua*), blue beech (*Carpinus caroliniana*), black gum (*Nyssa sylvatica*) and birch (*Betula nigra*) as the dominant species.

Peromyscus gossypinus and *P. nuttalli* were the dominant species of mammals present in the study areas. Other mammalian species present and occasionally caught were flying squirrels (*Glaucomys volans*), shrews (*Blarina brevicauda*) and house mice (*Mus musculus*).

The principal predators on the plots were moccasins (*Ancistrodon piscivorus*), copperheads (*Ancistrodon contortrix*), great horned owls (*Bubo virginianus*), barred owls (*Strix varia*), hawks (*Accipiter striatus* and *A. cooperii*), gray foxes (*Urocyon cinereoargenteus*) and minks (*Mustela vison*).

Precipitation was variable during the time the study was conducted. Rainfall amounted to 35 inches in 1955, 34.5 inches in 1956, and 74 inches in 1957. Average annual rainfall for the region was about 45 inches. No drastic extended temperature irregularities other than normal seasonal variation occurred during the time of the study.

METHODS

Two groups of mice were studied on two ecologically similar but separate study plots. Each of the plots was inhabited by both *P. gossypinus* and *P. nuttalli.* The two plots were about two miles apart on a direct line but considerably farther apart if natural dispersal routes of the two species were considered. This separation of the two plots was considered essential because the mice on one plot served as the experimental group, and the mice on the other served as the control group. Studies on these two plots covered a period from March 24, 1955, to March 23, 1958.

Each of the two study quadrats was surveyed in the form of a grid pattern composed of squares 75 feet by 75 feet in size. The control plot covered an area of 12.91 acres and the experimental plot embraced 13.04 acres. The small discrepancy in size between the two plots resulted from natural topographic features.

Each plot had live traps placed on it at the center of each of the 75 feet grids. The control plot contained 100 live traps and the experimental plot contained 101 live traps.

Nest boxes of the type described by Howard (1949) were also used on each of the plots. These boxes were alternately placed on the ground, or in trees or stumps to a distance of about six feet off the ground. The boxes were not utilized by the mice to the desired extent so that the majority of the data were obtained by the use of live traps. It was not possible to put the boxes in the ground as was done by Howard (1949) and Blair (1958) because of the high water

table in the area which caused the boxes to fill with water.

The trapping procedure on the two plots involved an intensive system of live trapping designed to capture and measure the population of mice living on each plot. The trapping procedure was the same on both plots. An exception to this was during the years 1957-58, when the control plot was periodically flooded by water and at these times traps were not set on this plot. Ordinarily, traps were set on each plot an average of 788 trap nights per month except August when no traps were set. As an additional check on the populations, all of the traps were set for continuous periods of five days during the months of March, June, September, and December. These five days of total trapping were followed by six days in which one-half the traps on each plot were set for three days. These were then closed and the remainder opened and set for three days. This over-all system of trapping was intensive enough, so that practically all the residents and a great majority of the transients were captured at one time or another. Gentry and Odum (1957) found that under ideal weather conditions only three nights of trapping were required to catch a resident population of rodents.

As each mouse was caught for the first time it was numbered by a system of toe clipping and ear punching, so that it could be recognized when it was recaptured. Records were kept of the species, age, sex, breeding condition, place caught and other pertinent information for each mouse. After a mouse was marked and examined, it was released at the site of capture.

When an adult male *gossypinus* was caught on the experimental plot for the first time, or when a juvenile or subadult male caught earlier reached sexual maturity, it was brought into the laboratory. Here 500r of x-irradiation was administered to the testes, with the rest of the body heavily protected by a lead shield. The irradiation was administered with a clinical x-ray machine operating at 79.2 KVP and five milliamperes at the rate of between 92r and 98r per minute. No filter was used.

Within 24 hours after being brought into the laboratory for treatment, the mice were returned to the experimental plot and released at the site of last capture. Male *gossypinus* from the control plot were also brought into the laboratory but these individuals were merely held for a 24 hour period before being released back into the population. This was done to eliminate any possible difference in reproduction on the two plots because of availability of male mice and to simulate experimental conditions.

The same procedure was carried out with respect to *nuttalli* males but irradiation of males of this species did not start until June 18, 1957.

Population Structure and Dynamics

Several aspects of the normal life history and population dynamics of the two species are important to a consideration of the effects of

irradiation. Consequently, several phases of the biology of these *Peromyscus* populations must be considered.

GENERAL POPULATION FLUCTUATIONS

It has been shown by several workers (Howard, 1949; Blair, 1951, 1953, 1958; McCarley, 1954a, 1958a and others) that rodent populations in North America are generally characterized by fluctuations in numbers of individuals from one season of the year to another. McCarley (1954a) and others have shown that *Peromyscus* populations in the southern part of the United States are characterized by low population numbers during the warmer months of the year and high population numbers during the cooler months. This seasonal fluctuation is apparently the result of an increase in reproduction which starts with the advent of cool nights in the fall.

A total of 168 individuals of both species were caught and marked on the control plot and a total of 273 individuals of both species were caught and marked on the experimental plot. Figure 1 shows the numbers of both species (including all age groups) caught or otherwise

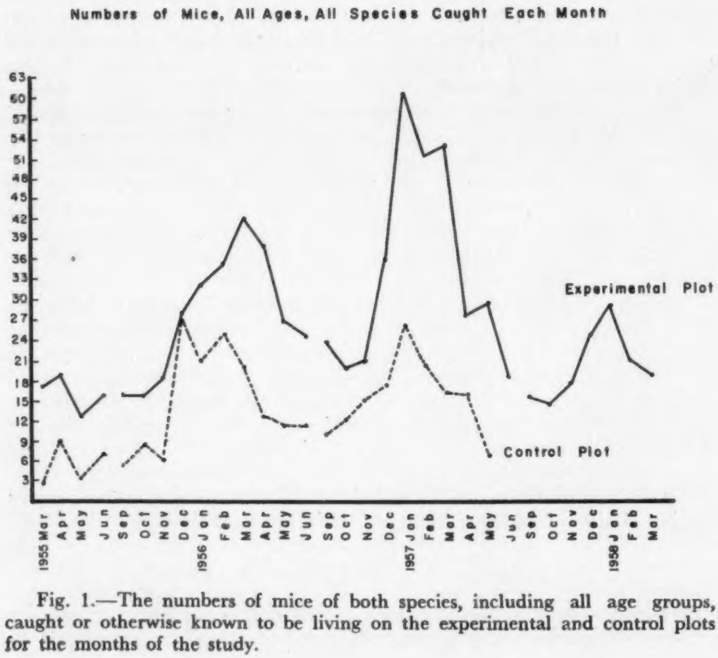

Fig. 1.—The numbers of mice of both species, including all age groups, caught or otherwise known to be living on the experimental and control plots for the months of the study.

known to be living on the two plots during the months of the study. The months of July and August were omitted because no trapping was done during August and the population in July was similar in structure and size to the June and September populations.

It can be seen in Figure 1 that during each month of the study the experimental plot supported a larger combined population of mice than did the control plot. This difference in mouse abundance apparently lay in ecological differences between the two plots. The dominant vegetation on both plots was similar but because of previous lumbering operations there were some differences in ecological succession between the two plots. The control plot was cut over some 30 to 40 years prior to the present study, so that the dominant vegetation present during the study was all second growth hardwood species. These trees had become large enough to form an almost complete overhead canopy, thus restricting the amount of sunlight that reached the forest floor. This created a more or less open vegetational community on the forest floor. The experimental plot was cut over in more recent years but the dominant vegetation was the same as that of the control plot. The stage of ecological succession was not so advanced, however. The trees on the experimental plot averaged 10.5 inches in diameter measured at breast height, while those on the control plot averaged 16 inches. The smaller trees on the experimental plot had not yet formed a complete canopy so that more sunlight reached the forest floor here than on the control plot. This condition produced, in some parts of the experimental plot, a rather dense growth of various species of oak and elm (*Ulmus* spp.) seedlings and saplings, rattan (*Berchemia scandens*), poison ivy (*Toxicodendron radicans*) and grapevine (*Vitis* sp.).

Apparently the comparatively greater amount of understory vegetation on the experimental plot formed a more favorable environment for the mice than that of the control plot. This resulted in a higher population density of mice per acre on the experimental plot than on the control plot. The correlation of higher population density with amount of underbrush has already been shown to exist for *P. nuttalli* (McCarley, 1958a).

It can also be seen in Figure 1 that the overall fluctuations in the two populations were generally parallel. It was pointed out earlier that this pattern of high population numbers during the cool months and comparatively low population numbers during the summer months was typical of rodent populations in the south.

The increase in population size which began in the late fall or early winter was the result of an increase in the reproductive rate. This was evidenced by the appearance of immature mice (Fig. 2 and Table I). At this time of the year the mortality rate was exceeded by the reproductive rate. This resulted in an increase in the proportion of immature mice to mature mice. At the beginning of the reproductive season, the populations of both species were composed of mature adults, most of which had been born late in the preceeding breeding

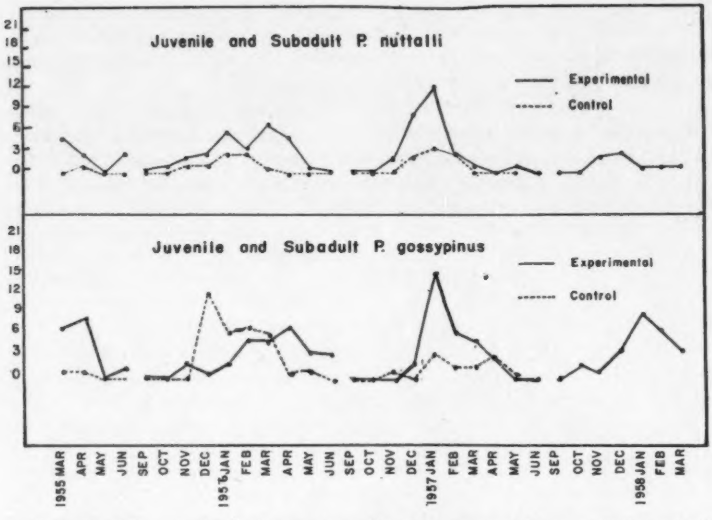

Fig. 2.—The numbers of immature *Peromyscus gossypinus* and *P. nuttalli* caught during each month of trapping for the months indicated.

season. In December, January, February, and March the populations were made up of a greater percentage of younger age classes than at other months of the year.

REPRODUCTION

A considerable amount of information has been published by Pournelle (1952) on the reproduction and early post-natal development of *gossypinus*. He reported that male mice generally became sexually mature and capable of inseminating females when they were between the ages of 45 to 70 days. During the summer months *gossypinus* males were generally sterile and Pournelle (*op. cit.*) attributed this sterility to the high average temperatures which prevailed during this time of the year in the south. Females became sexually mature, on the average, at about 43 days of age as indicated by the initial opening of the vaginal orifice. The gestation period varied from about 23 to 30 days with lactation apparently prolonging the gestation period. These facts agreed with field observations made during the present study.

No comparable studies have been made on the reproduction of *nuttalli*. Goodpaster and Hoffmeister (1954) reported one female *nuttalli* with a gestation period of 29 days. McCarley (1958a) showed that, in eastern Texas, *nuttalli* has essentially the same reproductive pattern as *gossypinus* and matures at about the same age.

The number of individuals produced in a litter by both species was somewhat variable. No females of either species ever gave birth to a litter in a nest box. The only evidence produced in this study that indicated the number of young in a litter was obtained from the autopsies of four pregnant females (three *gossypinus* and one *nuttalli*). Here, the number of embryos ranged from three to six. Pournelle (1952) found that the average size of *gossypinus* litters in Florida was 3.7 mice with a range of one to seven. No comparable information was available for *nuttalli*.

There is ample evidence to indicate that *gossypinus* does not form permanent mating bonds (McCarley, 1953; Bradshaw, 1957). The implication of this type of breeding relationship is that one male *gossypinus* would be likely to breed with several females during any one breeding season or even during one week.

Breeding relations in *nuttalli* were not so promiscuous as in *gossypinus*. This species apparently did tend toward temporary pairing during the breeding season as shown by the repeated capture of a male and female mouse in one restricted area. This type of behavior would tend to limit the reproductive activities of a male to

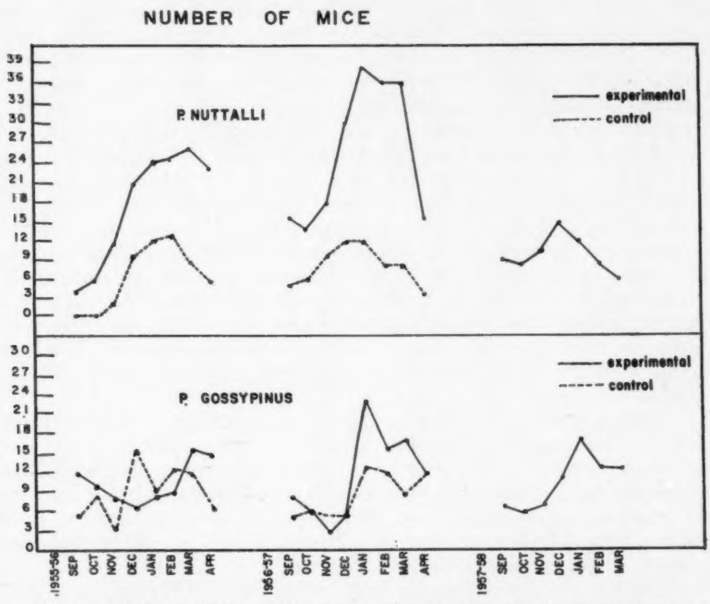

Fig. 3.—The numbers and fluctuations by species of all mice caught on the experimental and control plots during the three breeding seasons the study was in progress.

fewer females than would the promiscuous activity of *gossypinus* males.

Males and females of both species that were born early in the winter matured sexually during the same breeding season and usually became the parents of at least one litter during that particular breeding season. Those individuals that were mature adults at the beginning of a breeding season generally continued to breed throughout the breeding season. On several occasions, females of both species were known to be pregnant at least three times in one season.

Figure 3 shows the numbers and fluctuations by species of all mice caught on the two plots during the three breeding seasons the study was in progress. Because of differences in reproductive activities on the plots in different years, it was necessary to consider each breeding season separately.

Reproduction: 1955-56.—In September of 1955, the ratio of the *gossypinus* populations on the two plots was about the same as when the study started in March of 1955. The *gossypinus* population on the control plot increased in December as was expected and began a general decrease in the months of March and April. The increase in December was caused by two factors: (1) an increase in normal reproduction which produced at least nine juveniles that lived long enough to get caught in traps (Table I), and (2) an increase in dispersal of juveniles and subadults onto the plot from surrounding areas. These dispersing mice did not always establish home ranges on the plot, but at least they were present part of the time and consequently influenced the size of the population.

The *gossypinus* population on the experimental plot did not increase in the early winter but did increase in the months after January. This comparatively late increase in population size was almost entirely the result of dispersal onto the plot of juvenile and subadult mice from surrounding areas. Table I shows that probably none of the juvenile *gossypinus* appearing at this time were born on the plot. In this study the origin of juveniles on both plots was determined subjectively by the position on the plot where they were first caught and whether a suckling female had been in the area where the juveniles first appeared. Except in the cases indicated in Table I by a question mark, all juveniles caught on the experimental plot appeared first in peripheral traps.

During this breeding season there was, at all times on the experimental plot, a sufficient number of breeding males (all irradiated) and females in contact with each other to have normally produced more juveniles than apparently was the case. There were at least six pregnancies noted on the plot during this season, but none of these pregnancies definitely resulted in a litter of which any mice lived long enough to get caught in the traps.

The *nuttalli* populations on both the control and experimental plots increased in the expected manner during this breeding season. Figure 3 shows that the population curve of this species during this breeding season was comparatively smooth on both plots.

Table I.—Structure of breeding population of *P. gossypinus* on two study plots. Number of breeding condition (BC) females that were pregnant, shown in parentheses.

	EXPERIMENTAL							CONTROL						
	AD. ♂	AD. ♀	BC ♂	BC ♀	Total Juv.	Immigrant Juv.	Resident Juv.	AD. ♂	AD. ♀	BC ♂	BC ♀	Total Juv.	Immigrant Juv.	Resident Juv.
1955-56														
Sept.	7	5	6	4(0)	0	0	0	4	1	3	0(0)	0	0	0
Oct.	7	3	7	3(0)	0	0	0	7	1	7	1(1)	0	0	0
Nov.	4	2	4	2(1)	2	2	0	3	1	3	2(2)	0	0	0
Dec.	4	1	4	4(1)	1	1	0	4	1	4	1(1)	12	3	9
Jan.	5	2	5	1(0)	1	1	0	3	1	3	1(0)	3	3	0
Feb.	4	1	4	1(1)	2	2	0	5	1	5	1(0)	2	2	0
Mar.	6	5	6	5(2)	2	2	0	6	0	2	0(0)	1	1?	0
Apr.	7	1	6	1(1)	6	6?	0	5	1	0	0(0)	1	1	0
1956-57														
Sept.	2	5	2	4(1)	0	0	0	4	1	3	1(0)	0	0	0
Oct.	1	4	1	4(3)	1	1	0	4	2	4	2(2)	0	0	0
Nov.	1	2	1	2(2)	0	0	0	3	1	2	1(0)	0	0	0
Dec.	1	3	0	0(0)	2	2	0	4	1	4	1(0)	0	0	0
Jan.	1	7	1	7(5)	9	7	2	7	2	7	2(1)	2	2	0
Feb.	5	5	5	4(0)	2	2	0	5	5	5	4(1)	2	0	2
Mar.	5	7	0	6(3)	1	0	1	1	5	1	2(0)	1	1	0
Apr.	6	3	1	0(0)	1	1	0	2	6	0	0(0)	3	3	0
1957-58														
Sept.	2	5	2	3(0)	0	0	0							
Oct.	0	4	0	4(0)	1	1	0							
Nov.	0	6	0	5(1)	0	0	0							
Dec.	0	7	0	7(0)	2	0	2?				Flooded			
Jan.	3	5	3	5(0)	7	6	1							
Feb.	1	5	1	1(0)	3	3	0							
Mar.	3	6	1	0(0)	0	0	0							
Apr.	—	—	—	—	—	—	—							

There was some indication that dispersal of *nuttalli* onto the experimental plot was greater than on the control plot. Possible reasons for this may have been that the comparatively low *gossypinus* population created what might be called a population vacuum. This produced more available home sites or "spaces" for dispersing mice to occupy than would have been the case had the experimental *gossypines* reproduced at a rate comparable to that on the control plot.

During this breeding season there was little or no successful reproduction of *gossypinus* on the experimental plot. The overall size of the combined experimental *gossypinus* and *nuttalli* populations (Fig. 1) was maintained by dispersal onto the study plot of immature mice of both species.

The comparative overall difference between the size of the 1955-56 *gossypinus* population on the experimental plot and that of the control plot was greater than the difference between the two populations which existed at the time the study began. In the spring of 1955 there was an overall ratio of two control *gossypinus* to three experimental *gossypinus*. Using a chi-square test based on this two to three ratio, the 1955-56 *gossypinus* population on the experimental plot was significantly smaller than the 1955-56 *gossypinus* population on the control plot. In this case chi-square equaled 10.74.

Reproduction: 1956-57.—The increase of the *gossypinus* population on the experimental plot during this breeding season took place earlier in the fall than in the previous year. The increase of juvenile mice in the population began in December instead of January (Fig. 2, Table I). Of the 16 juveniles trapped during this entire breeding season, however, only three or 19 percent were the probable offspring of resident females. There were very few males on the plot during this season (Table I). In spite of the small percentage of males caught on the plot there were 14 known pregnancies in females living there during this breeding season. Some, but not all, of these females could have bred with irradiated males as indicated by the location of their home ranges. Because of the low number of males, most of the females probably bred with males living outside the periphery of the plot. These males would not have been caught and consequently not irradiated. The low number of resident juvenile mice (Table I) indicated that some of these females probably had home ranges which were largely out of the limits of the study area, or that other unknown factors were responsible for the scarcity of juveniles.

The low number of resident juvenile mice on the experimental plot during this breeding season indicated that there was very little successful reproduction involving study plot males and females. A comparison between the control and experimental *gossypinus* populations for this breeding season was not justified because of the low number of breeding females on the control plot.

Because of dispersal onto the plot of young *gossypinus* from surrounding areas, the level of the experimental *gossypinus* population remained high.

The *nuttalli* populations on both plots followed the expected pattern with most of the increase in juveniles coming from successful reproduction on the plots and comparatively little from dispersal from surrounding areas.

Reproduction: 1957-58.—Reproduction of experimental *gossypinus* during the 1957-58 season was similar to the previous season. Again, there was a marked absence of male *gossypinus* on the experimental plot. This lack of males may, in part, be the cause of the low number of pregnancies observed on the plot during this season. This seems doubtful, however, in view of the number of pregnancies recorded the previous season on the same plot, when a low adult male *gossypinus* population was also observed. Comparisons with the control plot were of no value at this time since this plot was subjected to periodic flooding which decimated the population (McCarley, 1959). There was an extremely low number (one) of *gossypinus* pregnancies this year as compared to past years. A maximum of three juvenile mice, apparently from the one pregnancy, were born on the plot and lived long enough to get caught. Because of dispersal of younger age classes onto the plot, no significant differences were observed between the population level at this season and the levels of the previous two seasons.

The 1957-58 season marked the first x-ray treatment of male *nuttalli*. The fluctuations and numbers of experimental *nuttalli* as shown by Figure 3 were roughly comparable during 1955-56 and 1956-57. At least there was no significant difference between the two populations as indicated by the "t" test. Figure 3 shows that during the 1957-58 breeding season the *nuttalli* population on the experimental plot did not increase as it had in the two previous years. Almost no breeding of *nuttalli* occurred on the plot during this season as indicated by the low number of juveniles (Fig. 2). During this season six adult males in breeding condition, and an average of five females a month from September through March, were present at various times. Only one of these females was ever noted as being pregnant although all were continually in breeding condition as indicated by the vaginal opening. All indications were that there was no successful reproduction of *nuttalli* on the experimental plot during this season. No more than normal dispersal of young *nuttalli* onto the plot occurred as compared to the pattern of the previous two years. The overall result was a low *nuttalli* population density.

The apparent decrease in size of the *nuttalli* population on the experimental plot when compared with the previous two seasons was of statistical significance. The 1957-58 experimental *nuttalli population* was highly significantly lower than the 1956-57 experimental population, and the 1957-58 experimental population was significantly lower than the 1955-56 experimental population according to the "t" test. As previously indicated, no significant difference was noted between the 1955-56 and 1956-57 *nuttalli* populations on the experimental plot. There were too few *nuttalli* trapped on the control plot during all of

these breeding seasons to warrant a chi-square test between the control and experimental areas for this species.

LONGEVITY

Mice of the genus *Peromyscus* have considerably shorter life spans in the wild than their potential life spans as measured by the time these mice may live in captivity. This is true because they form the basic food of many predators.

To find out the average length of life span in the wild of *gossypinus* and *nuttalli,* several factors had to be considered. The most important factor was that when a mouse disappeared from the plots, or at least was not caught for several months, there was no positive assurance that this mouse was dead. The mouse may simply have moved to another area. The fate of the majority of the mice that disappeared could never be definitely ascertained unless they were found dead in a trap. It was known, however, that ordinarily when a mouse was caught within a particular group of traps over a period of time, that mouse would generally stay in that area so long as it was alive. Prior to the establishment of a home range a mouse was generally considered a transient or migrant.

In this study a mouse must have established a residence on the plots before it was eligible for consideration in the calculations of life spans. The criteria used to distinguish transient from resident mice were that if a mouse was caught two or more times in one area it was considered a resident, but if it was caught only two times, the times of capture must have been at least 20 days apart. It was believed that these criteria eliminated from consideration those transient individuals that were simply moving through the plots.

Another factor that required consideration was the age of a mouse when it was first captured. Condition of the pelage and size of the mouse were the two criteria used to determine age. If a mouse of either species was caught showing juvenile pelage conditions, it was considered to be at least 25 days old (see Pournelle, 1952, McCarley, 1958a, for the basis of this reasoning). If a mouse was caught showing subadult pelage color, it was assumed that its minimum age was at least 35 days. Adults were distinguished, not only by pelage color, but by larger size and sometimes by whether or not they were sexually mature as evidenced by the external appearance of the reproductive organs. An adult was considered to be at least 60 days old.

The life spans of the mice were calculated in the following manner: assume that a mouse was first caught as an adult. This meant that this particular mouse was at least 60 days old. Over a 93 day period it was caught seven times which established it as a resident. After 93 days it was not caught again. Thus it can be assumed that when this mouse disappeared it was at least 153 days old or approximately 5.01 months (153/30.5 days). This would be called the minimum life span of that mouse (McCarley, 1958a).

It was impossible, using traps alone, to capture the very young individuals before they left the nest. Because of the omission of these young mice from the analyses, the minimum life spans given below are undoubtedly longer than would be the case if these very young mice had been considered.

Figure 4 shows the results of calculations of average minimum life spans by age classes for each species on each study plot. Figure 4 was constructed by the method described originally by Dice and Leraas (1936), and modified by Hubbs and Hubbs (1953). There were too few subadults and juveniles to consider separately, hence they were grouped together as immatures. The small discrepancies in average life spans of *nuttalli,* as shown by Figure 4 and the data presented by McCarley (1958a), can probably be attributed to the smaller sample available from which the 1958a data were derived.

Figure 4 shows that there were no striking differences in life spans of mice on the control plot and mice on the experimental plot. There was some indication that *nuttalli* on both plots lived longer than *gossypinus* on both plots but this difference was not significant. The large

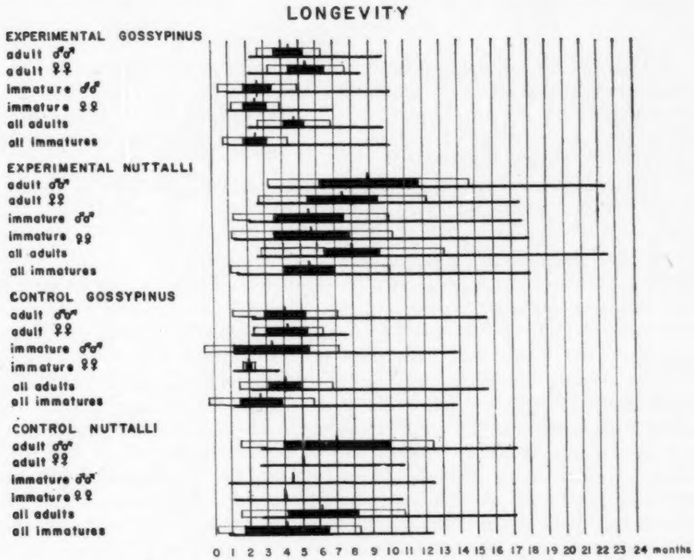

Fig. 4.—Variation in longevity of *P. gossypinus* and *P. nuttalli* on each of the study plots by sex and age group. The range of variation for each group is shown by the heavy horizontal line. The blackened part of each bar comprises two standard errors of the mean on either side of the mean (narrow triangle). One-half of each black bar plus the white bar at either end outline one standard deviation of the mean.

standard deviations of almost every age class (Fig. 4) indicated that there was a wide deviation of ages from the mean.

There were no significant differences between life spans of *gossypinus* and *nuttalli* on either of the plots. It does appear (Fig. 4) that experimental adult *gossypinus* differed significantly from experimental adult *nuttalli,* but this difference was not significant when a comparison was made with a "t" test.

As indicated by the position of the means there was some difference in longevity between adults and immatures of both species on both plots. There was significant difference, however, only between adult male and female *gossypinus* on the experimental plot and immature male and female *gossypinus* on the same plot. The difference between adult *gossypinus* males and immature *gossypinus* males was significant, and the difference between adult *gossypinus* females and immature *gossypinus* females on the same plot was highly significant. When all of the experimental adult *gossypinus* were grouped together and compared with the lumped experimental immature *gossypinus,* the difference was highly significant by a "t" test.

DISPERSAL

Dispersal in animal populations is usually a characteristic that is most pronounced in the younger age classes. It has been shown by several workers (particularly Howard, 1949; Blair, 1951) that mature mice have a tendency to remain in the same area, once they have established a home range.

In the present study there was no way of determining the distance or rate at which the younger age classes dispersed. This was primarily the result of not knowing the precise origin of a litter or of an individual. The only trapping that was done outside the confines of the study areas was between the two plots to see whether or not there was any exchange of mice between the two plots. No marked mice were ever recovered over 100 yards from either of the two plots. This was suggestive that dispersal off the plots was not extensive.

There was, however, considerable evidence to indicate that mice that were not born on the plots were constantly dispersing onto the study plots, especially on the experimental plot. This was particularly true of the immature age classes and to a lesser extent of adults. The information given in Table I shows that on the experimental plot the majority of the juvenile mice that appeared in traps probably came from some place other than the study plot proper. This was also true to a lesser extent on the control plot.

It was likely that all of the mice which were first caught as subadults on both plots were immigrants onto the plots from surrounding areas. The reason for this was that there was a 10-15 day period from the time a juvenile mouse left the nest until it began to have pelage changes indicating subadult age. During this period the mice were subject to capture. At the time of the year when the younger

age classes were appearing, traps were always set at least four nights in any 15 day period. This was an adequate number of trap nights, with the number of traps used, to have caught practically all juvenile mice that were living on the plots.

The movement of *gossypinus* onto the study plots was greater than the movement of *nuttalli* onto the plots. This fact was revealed by two things. Practically all juvenile *nuttalli* that were captured on either of the two plots could be assigned as offspring of definite resident females, and most of the juvenile *gossypinus* had an unknown origin. There were also comparatively few *nuttalli* individuals caught for the first time as subadults on either plot.

Dispersal or immigration of subadults of both species onto the experimental plot was also much higher than on the control plot. On the experimental plot subadults made up 25 percent of the total mice caught of both species. On the control plot, however, the number of subadults of both species was 14 percent. This indicated a much higher influx of subadult animals onto the experimental plot than on the control plot. It would follow that the size of the population on the experimental plot was maintained more by dispersal than was the size of the population on the control plot.

Home Ranges

The home range of an animal is generally defined as that area over which an animal roams in its normal search for mates and the requirements of existence. It is generally recognized that the methods currently in use make it almost impossible to get an absolute measure of size of home range by traps alone (Hayne, 1949; Stickel, 1954). Any home range figure derived from trap data is, at best, only an estimate of the area an animal covers but the figure is useful for comparative purposes.

Estimates of home ranges in this study were made from trap data by the method proposed by Blair (1940) and described by Stickel (1954) as the "inclusive boundary strip method." This method assumes that the home range of an animal may extend beyond the traps in which it was caught so that one-half the distance to the next trap would be included in the calculations.

The grid pattern and spacing of the traps have already been discussed. It should be mentioned that in most cases the traps were not placed precisely beside the stakes which indicated 75 feet between traps, but anywhere within a four-to-five foot radius of the stakes and in positions most likely to catch mice. The trapping procedure was varied in several manners such as setting every other trap and alternating rows of traps after several nights in which all traps were set. This was done to eliminate the constant recapture of one particular individual in a trap, when this trap happened to be near the nest or home-site of the mouse. In addition, if a mouse was caught two trap

nights in succession in the same trap, that trap was then closed for a night.

Certain mice were excluded from the calculations. These were individuals caught less than three times and immature individuals which may have been captured three or more times but which were obviously wandering around without any definite home range. Also excluded were the occasional, and usually obvious, travels made by a mouse outside a normal established home range. In a few cases the periods of observation were of long duration and it was necessary to exclude from home range estimates those individuals which changed their home ranges. This was a rare occurence and was always obvious in the raw data so that no problem was posed by this factor.

Haugen (1942) and Blair (1942) have showed that it was necessary to capture a small mammal about ten or more times before it was possible to have an accurate estimate of the maximum home range. Because traps were not set continuously in this study, only a few individuals were caught that many times.

TABLE II.—The average size of home ranges of male and female *P. gossypinus* from the experimental plot according to the number of times captured. Number of individuals shown in parentheses

No. of Captures	Male	Female
3	.54 (22)	.41 (21)
4	.62 (22)	.55 (21)
5	.79 (22)	.61 (21)
6	.93 (17)	.70 (18)
7	.94 (14)	.90 (13)
8	1.03 (14)	1.04 (12)
9	1.24 (11)	1.26 (11)
10	1.16 (6)	1.37 (10)
11	1.44 (5)	1.41 (10)
12	1.57 (5)	1.84 (6)
13	1.76 (4)	1.93 (4)
14	1.66 (3)	1.93 (4)
15	1.98 (3)	2.17 (3)

Table II shows the average home ranges in acres of male and female *gossypinus* from the experimental plot according to the number of times captured. The home range size generally increased in both sexes with the number of captures. There were no significant differences between home ranges of males and females on this plot at any level of captures. Too few *gossypinus* were captured enough times on the control plot to give anything but a rough estimate of home range size on this plot. Eight males and eight females captured eight times each on the control plot had averaged home ranges of $2.26 \pm .29$ acres and $1.48 \pm .30$ acres, respectively. There was no significant difference between these two figures.

If the home ranges of all adult *gossypinus* caught eight times on

the control plot were compared with the home ranges of all adult *gossypinus* caught eight times on the experimental plot, it was found that the control plot *gossypinus* had average home ranges of $1.87 \pm .22$ acres and the experimental plot *gossypinus* had average home ranges of $1.17 \pm .09$ acres. These average home ranges were not significantly different when tested by a "t" test.

McCarley (1958a) showed that *nuttalli* on the experimental plot captured ten or more times had no significance between home ranges of males and females. Males averaged $1.46 \pm .17$ acres and females averaged $1.40 \pm .22$ acres. There were too few *nuttalli* captured on the control plot to make any comparison with experimental *nuttalli*. The apparent size of home range of *nuttalli* in this study was considerably larger than the home range size of this species reported by Sealander and Redman (1958) in Arkansas. The small home range size reported by Sealander and Redman (*op. cit.*) was apparently the result of a low number of captures and small size of the study plots.

The largest home range encountered in either species was that of an adult male *gossypinus* captured 25 times on the control plot with a calculated home range of 4.46 acres.

Table III.—The number of individuals of each sex for the three age classes of *P. gossypinus* and *P. nuttalli* caught on the control and experimental plots over a three-year period (1955-1958)

Species	EXPERIMENTAL Male	Female	CONTROL Male	Female
gossypinus				
adults	43	35	49	17
subadults	28	12	8	7
juv.	22	22	16	12
nuttalli				
adults	25	27	22	16
subadults	12	16	4	3
juv.	16	14	6	3

Sex Ratios

Table III shows the number of mice by sex, species, and age class that were caught on the plots during the course of the study. The only significant deviations from an expected 1.1 ratio were between adult male and female *gossypinus* on the control plot and subadult male and female *gossypinus* on the experimental plot. The departure of adult male and female *gossypinus* from the expected 1.1 ratio gave a chi-square value of 14.56 which was highly significant. The deviation in subadult male and female *gossypinus* gave a chi-square value of 5.62 which was significant. This imbalance of sexes in this study was probably the result of the fact that males were inclined to roam

more extensively than females and consequently more likely to be caught (Hays, 1958).

MUTATIONS

This particular study was not designed to detect phenotypic expressions of mutations. However, on the basis of the work of Russell (1954 and later), it was expected that the mutation rate would be raised by the x-irradiation. The reasons why there was such a small chance of observing phenotypic expressions of radiation induced mutations in natural populations have already been set forth by Muller (1954) and will not be repeated at this time.

Two instances of possible phenotypic expressions of mutations were noted in *Peromyscus gossypinus*. This species is ordinarily a rich mahogany brown color on the dorsal surface and the entire ventral surface is a pale cream or whitish color. In January of 1957, several individuals on the experimental plot were noticed with various degrees of brown spotting on the ventral surface. After this apparent abnormality was noted, all *gossypinus* on both plots were closely checked. This intensive checking revealed that an additional pelage aberration was sometimes present. This consisted of white hair covering the last five millimeters of the dorsal surface of the tail. (The ventral surface of the tail was ordinarily covered with white hair). Sometimes this white-tail tip was associated with the brown spotting and sometimes it was not, but there were too few instances to determine whether any definite pattern of occurrence was present.

Forty-two individuals were examined on the control plot during and subsequent to January of 1957, and it was found that four (9.5%) of these individuals had either the brown spotting, white-tail tip or a combination of both. An examination of 73 individuals on the experimental plot during and subsequent to January, 1957, showed that 15 (20.5%) of these individuals had the brown spotting, white-tail tip or both. This was a considerably higher rate of occurrence than on the control plot. As an additional check 79 study skins of *P. gossypinus* collected elsewhere in eastern Texas were examined. It was found that about ten percent of these individuals also had the spotting, white-tail or both. This indicated that this pelage aberration was normally found in *gossypinus* populations in eastern Texas. It appeared that in a normal Mendelian population of *gossypinus* these slight abnormalities occurred in about 10 percent of the total population. The higher rate of occurrence (20.5%) on the experimental plot was highly significant when compared with the apparently normal 10 percent occurrence (chi-square was equal to 11.11 in this case). No other visible morphological deviations were noted in either *gossypinus* or *nuttalli* on either of the two plots.

DISCUSSION AND CONCLUSIONS

Peromyscus gossypinus and *P. nuttalli* should be regarded as species that are reasonably well adapted to the environment in which they

live. In spite of seasonal fluctuations in numbers and varying pressures of natural selection, the over-all gene combinations of the two species are apparently in equilibrium with the environment. Because irradiation would produce an increase in genetic variation, it is likely that x-ray treatment would tend to upset this presumed equilibrium thereby reducing, rather than increasing, the adaptability of the species.

The details of the genetic effects that were presumed to have been produced in these mice by irradiation could not be detected by the methods or techniques used. Fortunately, the work of Russell (1954, 1956) on laboratory populations of mice (*Mus musculus*) showed that an x-ray dosage of the magnitude used in this study would cause a considerable number of mutations to occur in the germ cells. Consequently, a considerable number of mutations can be assumed to have been produced in the irradiated males in this study.

Russell (1956) has reviewed evidence which showed that male mice which were exposed to an acute dose of several hundred roentgens remained fertile for about four or five weeks after irradiation. During this period the number of inheritable changes in the gametes was extremely high. The reason for this was that gametes produced immediately after irradiation were in the post-spermatogonial stage at time of irradiation. The four to five week period of fertility was followed by a period of sterility, the length of which apparently depended on the amount of ionizing radiation received by the gonads (Strandskov, 1932). This period of temporary sterility was a result of killing the spermatagonia which were present at the time of irradiation and which were especially sensitive. Return of fertility took place when an adequate replacement of the killed spermatagonia had occurred.

Russell (1954) and Muller (1954) have reviewed the types of genetic changes which resulted from ionizing radiation. They have shown that offspring produced from matings which occurred during the pre-sterile period showed a high incidence of dominant effects. These effects were most noticeable in the form of prenatal lethality, partial sterility, and total sterility.

These dominant effects were either absent, or greatly reduced, in offspring resulting from matings which took place after the sterile period (Russell, 1956). The genetic effects produced in offspring at this time were largely recessive in nature. Russell also made the point that there was no difference in the incidence of mutations transmitted at a time immediately following recovery of fertility and a time some months later.

Forty-five male *gossypinus* were irradiated between June 22, 1955 and January 21, 1958. Each of these males lived on the plot an average of slightly over four months. It would be expected that during this time, these males would have transmitted a large number of mutated genes to the remainder of the population. This would be ex-

pected because of the promiscuous breeding behavior exhibited by this species.

The significantly smaller *gossypinus* population on the experimental plot during the breeding season of 1955-56 (when compared with the control plot population) was probably a direct result of the x-irradiation. The irradiation factor was the only environmental influence of any significance that differed between the two plots at this time. The assumption that radiation affected reproduction in *gossypinus* was supported by the following: All seven of the male mice living on the plot in September, 1955, were irradiated in September. On the basis of the information presented above we can assume that during September, these male mice were fertile, or at least partially so. In addition, this was the period in which the gametes were most likely to be carrying gross chromosomal changes which would probably result in high prenatal and immediate postnatal lethality. These seven mice were probably sterile during October. It can be assumed that they probably began to recover their fertility sometime in November or December, although only two of seven mice were still being caught in November. An additional three mice were irradiated in October. This meant that the majority of all male mice living on the plot during the early fall of 1955 were either in the very critical pre-sterile period or were sterile. Either condition would be expected to cause a reduction in the number of juvenile mice born on the plot which would live long enough to get caught in traps. Blair (1958) reported that a similar dosage of x-irradiation caused a significant decrease in litter size in *Peromyscus maniculatus* in Central Texas.

Consequently the lack of production of juveniles during the 1955-56 season (see Table I) is attributed to conditions which were caused by the irradiation. It seems likely that the main influencing factor was sterility of the males and production of prenatal and postnatal lethal mutations.

It has been shown earlier that during the breeding seasons of 1956-57 and 1957-58, there was a relatively small amount of successful *gossypinus* reproduction on the experimental plot. The size of the population, however, was maintained by dispersal of mice onto the area of study. Lack of reproduction during these two seasons was attributed to the factors mentioned above and to the deleterious action of mutations which were probably carried by some of the mice in a heterozygous condition. Russell (1956) pointed out that many radiation induced mutations did have harmful effects in the heterozygous condition.

The significant decrease of the experimental *nuttalli* population during the 1957-58 breeding season can probably be attributed to the same irradiation factors that accounted for the lack of reproduction in the experimental *gossypinus* during the fall of 1955. The situations were very similar with regard to number of males present and times of irradiation.

It was stated earlier that most of the juveniles and subadults which

were caught on the experimental plot were immigrants into the area and not the offspring of resident mice. It would seem that this constant immigration of new mice into the study area would tend to offset any over-all deleterious effects in future generations. It should be remembered, however, that the populations of mice on both plots were parts of a larger, more or less continuously distributed, population. It is as reasonable to assume that radiated *gossypinus* males living near the periphery of the study areas reproduced as much with *gossypinus* females off the plots as with females on the plots. This would mean that normal gene drift would tend to spread mutated genes over a wider area than that of the study plot proper. This was most certainly true by the end of the breeding season of 1956-57. The assumption was made that at least some of the mice dispersing onto the experimental plot had an irradiated male for an ancestor and that some of these immigrant individuals carried deleterious genes which resulted from the irradiation.

There was evidence that the life spans of the offspring of irradiated male *gossypinus* were shorter than would ordinarily be the case. It has been pointed out that the only significant differences between life spans of adults and immatures of either species on either study plot was between adult and immature *gossypinus* on the experimental plot. In spite of the fact that it was impossible in this study to know which juveniles were the offspring of radiated males it was reasonable to assume that a large percentage of the juveniles were either directly or indirectly the offspring of irradiated males. If this was true, then it would be expected that some of these offspring would be carrying deleterious genes which were the direct result of the irradiation of some of their ancestors. These genes, which would probably put the animals at a selective disadvantage, even in the heterozygous condition, could account for the significant differences in life spans of experimental adult and immature *gossypinus* (Russell, 1957). The assumption is made that while natural selection operates equally on both young and old age classes, the most critical time for survival is when the mice are young. Most of the selection against deleterious gene combinations would probably be made in the younger age classes.

The pelage mutations which were discussed were probably caused by genes which did not seriously affect the survival of the affected individuals. It may be presumed that this pelage trait was caused by a gene or genes which were normally present in the populations and which were probably inherited in some recessive manner. The brown spotting of the ventral surface has also been observed by McCarley (unpublished data) in *Peromyscus leucopus* and the white-tail tip in *Rattus norvegicus*. The higher rate of occurrence in the irradiated experimental *gossypinus* indicated that the gene or genes causing this abnormality were susceptible to the effect of the x rays. This could account for the significantly higher rate of occurrence of this pelage character in irradiated than in non-irradiated *gossypinus*.

There was no indication that size of home range was affected either

directly or indirectly by the irradiation. The disparity in sex ratio from an expected 1:1 was attributed to natural behavior of the species.

SUMMARY

The dynamics of two populations of *Peromyscus gossypinus* and *Peromyscus nuttalli* were studied for 37 months on 13 acre study plots located in a floodplain forest habitat in eastern Texas. Male mice of both species from the experimental population were treated with 500r of x-irradiation, administered to the testes, and released back into the population.

There was evidence to indicate that irradiation decreased the reproductive rate through a decrease in number of litters or size of litters. The life spans of presumed offspring of irradiated *P. gossypinus* were significantly shorter than the life spans of presumed offspring of non-irradiated individuals. The irradiated population also exhibited a significantly larger incidence of a pelage color mutation.

In spite of the deleterious effects of the x-irradiation on the populations, the over-all size of the irradiated populations was maintained by an increase in dispersal of immigrant mice (largely subadults) onto the study plot where the irradiated population was living.

REFERENCES

BLAIR, W. FRANK 1940—Home ranges and populations of the meadow mole in southern Michigan. Jour. Wildl. Manag., **4**:149-161.

———1942—Size of home range and notes on the life history of the woodland deer mouse and eastern chipmunk in northern Michigan. Jour. Mamm. **22**:148-157.

———1951—Population structure, social behavior, and environmental relations in a natural population of the beach mouse *(Peromyscus polionotus leucocephalus)*. Contr. Lab. Vert. Biol., Univ. Mich. **48**:1-47.

———1953—Population dynamics of rodents and other small mammals. Adv. in Genetics. **5**:1-41.

———1958—Effects of irradiation on a natural population of the deer mouse *(Peromyscus maniculatus)*. Ecology **39**:113-118.

BRADSHAW, W. N. 1957—Isolating mechanisms in the *Peromyscus leucopus* species group of mice. Unpub. M. A. Thesis, Univ. Texas, Austin.

DICE, LEE R. AND HAROLD J. LERAAS 1936—A graphic method for comparing several sets of measurements. Contr. Lab. Vert. Gen., Univ. Mich. **3**:1-3.

GENTRY, J. B. AND EUGENE P. ODUM 1957—The effect of weather on the winter activity of old-field rodents. Jour. Mamm. **38**:72-77.

GOODPASTER, W. W. AND DONALD F. HOFFMEISTER 1954—Life history of the golden mouse, *Peromyscus nuttalli* in Kentucky. Jour. Mamm. **35**:16-27.

HAUGEN, A. O. 1942—Home ranges of cottontail rabbit. Ecology **23**:354-367.

HAYNE, DON W. 1949—Calculation of size of home ranges. Jour. Mamm. **30**: 1-18.

HAYS, HORACE A. 1958—The distribution and movements of small mammals in central Oklahoma. Jour. Mamm. **39**:235-244.

HOWARD, WALTER E. 1949—Dispersal, amount of inbreeding and longevity in a local population of prairie deer-mice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol., Univ. Mich. **43**: 1-50.

HUBBS, CARL L. AND CLARK HUBBS 1953—An improved graphical analysis and comparison of series of samples. Syst. Zool. **2**:49-57.

McCARLEY, W. H. 1953—Biological relationships of the *Peromyscus leucopus* species group of mice in eastern Texas. Unpublished Ph.D. thesis, Univ. of Texas, Austin.

———1954a—Fluctuations and structure of *Peromyscus gossypinus* populations in eastern Texas. Jour. Mamm. **35**:526-532.

———1954b—The ecological distribution of the *Peromyscus leucopus* species group in eastern Texas. Ecology **35**:375-379.

———1958a—Ecology, behavior and population dynamics of *Peromyscus nuttalli* in eastern Texas. Tex. Jour. Sci. **10**: 147-171.

———1959—The effect of flooding on a marked population of *Peromyscus gossypinus* and *P. nuttalli*. Jour. Mamm. **40**: in press.

MULLER, H. J. 1954—The nature of the genetic effects produced by radiation. *In* Hollaender, *Radiation Biology*, Vol. I, Part 1, McGraw-Hill Book Co., New York.

POURNELLE, GEORGE H. 1952—Reproduction and early post-natal development of the cotton-mouse, *Peromyscus gossypinus*. Jour. Mamm. **33**: 1-20.

REDMAN, JOHN P. AND JOHN A. SEALANDER 1958—Home ranges of mice in southern Arkansas. Jour. Mamm. **39**:390-395.

RUSSELL, W. L. 1954—Genetic effects of radiation in mammals. *In* Hollaender, *Radiation Biology*, Vol. I, Part 2, McGraw-Hill Book Co., New York.

———1956—Genetic effects of radiation in mice and their bearing on the estimation of human hazards. Proc. Int. Conf. on Peaceful Uses of Atomic Energy, Geneva, 1955. Vol. **11**:382-383, 401-402.

———1957—Shortening of life in the offspring of male mice exposed to neutron radiation from an atomic bomb. Proc. Nat. Acad. Sciences **43**:324-329.

STICKEL, LUCILLE F. 1954—A comparison of certain methods of measuring ranges of small mammals. Jour. Mamm. **35**: 1-15.

STRANDSKOV, H. H. 1932—Effects of X-rays in an inbred strain of guinea pigs. Jour. Exp. Zool. **63**: 175-202.

Key and Notes to the Anoplura of Minnesota[1]

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This key deals with the adult sucking lice which are found on mammals in Minnesota. Although primarily restricted to Minnesota lice, the key can be extended to sucking lice which may be found on mammals in the north-central region. The key covers all sucking lice known or suspected to occur in Minnesota. The suspect-species were obtained from records of louse-host associations of other areas. If a louse occurred on a mammal from another area and the host was represented in this area, it is assumed that this louse-host association may occur in Minnesota. Records of mammals found in Minnesota were obtained from Gunderson and Beer (1953).

The couplets are based upon characters which can be located easily and readily distinguished from their couplet counterparts. Thus workers, who are not familiar with entomological terminology, can use the key and arrive at a specific determination with confidence. Specific descriptions of lice and references to louse-host associations may be obtained from Ferris (1916, 1919-1935, 1951, 1953), Hopkins (1948) and Kellogg and Ferris (1915).

The key is based solely on adult characters and holds for both males and females unless otherwise specified. Plate I, a labeled generalized louse, should familiarize readers with the major terms used in this key. Drawings are used to illustrate specific characters which

TABLE I.—Number of known and suspected louse-host associations in Minnesota

Host order	Mammal species in Minnesota	Known or suspected to harbor lice	Known to harbor lice in Minnesota
Chiroptera	7	0	0
Insectivora	8	1	0
Carnivora	22	4	2
Rodentia	27	23	13
Sciuridae	11	11	7
Heteromyidae	1	1	1
Cricetidae	12	8	4
Muridae	3	3	2
Lagomorpha	3	3	0
Perissodactyla	2	2	2
Artiodactyla	9	5	5
Primates	1	1	1
Total	106	62	37

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TABLE II.—Numerical associations of genera and species of lice known or suspected to occur in Minnesota

Lice Genera	Number of species known or suspected	Number of species known
Enderleinellus	4	1
Eulinognathus	1	0
Fahrenholzia	1	1
Haematopinoides	1	0
Haematopinus	3	3
Haemodipsus	2	0
Hoplopleura	6	5
Linognathus	5	4
Microphthirus	1	1
Neohaematopinus	3	3
Pediculus	1	1
Polyplax	4	2
Pthirus	1	1
Solenopotes	2	1
Total	35	23

are employed in key-couplets. These figures are arranged so that the anterior part points toward the top of each plate. Small arrows, on or near the figures, point to the couplet characters under consideration.

An asterisk following a species name denotes that the louse has been collected in Minnesota. The absence of an asterisk designates the louse as a suspect-species.

Possible mammalian louse-hosts are included in eight orders in Minnesota. Lice have been collected from various species in five of the eight orders (Table I).

There are fourteen genera of lice known or suspected to occur in Minnesota. Representatives of all but three have been collected. The latter are *Eulinognathus* which is found on the black rat, *Haematopinoides* from the prairie mole and *Haemodipsus* from domestic and wild rabbits. Records show that twenty-three of thirty-five species of lice known or suspected to occur in Minnesota have been collected (Table II).

NEW MAMMAL-LICE ASSOCIATIONS

Several new associations between sucking-lice and mammals are listed below. The associations of *F. pinnata* K. & F. with the pocket mouse, *M. uncinatus* (Ferris) on the southern flying squirrel and *H. setoni* Ewing on the varying hare are reports not previously recorded. The other associations are new for Minnesota. The host species were identified by J. R. Beer and the louse species by E. F. Cook.

Host: *Synaptomys borealis* (Richardson) — Lemming mouse. Collected by J. R. Beer, Basswood Lake, Lake Co., Minnesota.
Louse: *Hoplopleura acanthopus* (Burmeister)

Host: *Perognathus flavescens* (Merriam) — Pocket mouse. Collected by J. R. Beer, Rosemount, Dakota Co., Minnesota.
Louse: *Fahrenholzia pinnata* Kellogg and Ferris

Host: *Glaucomys volans* (Linnaeus) — Southern flying squirrel. Collected by L. D. Frenzel, Cedar Creek, Minnesota, December, 1956.
Lice: *Hoplopleura trispinosa* Kellogg and Ferris
Microphthirus uncinatus (Ferris)
Neohaematopinus sciuropteri (Osborn)

Host: *Lepus americanus* (Erxleben) — Varying hare. Collected by C. C. Loan, Rampart House, Yukon, Canada.
Louse: *Haemodipsus setoni* Ewing

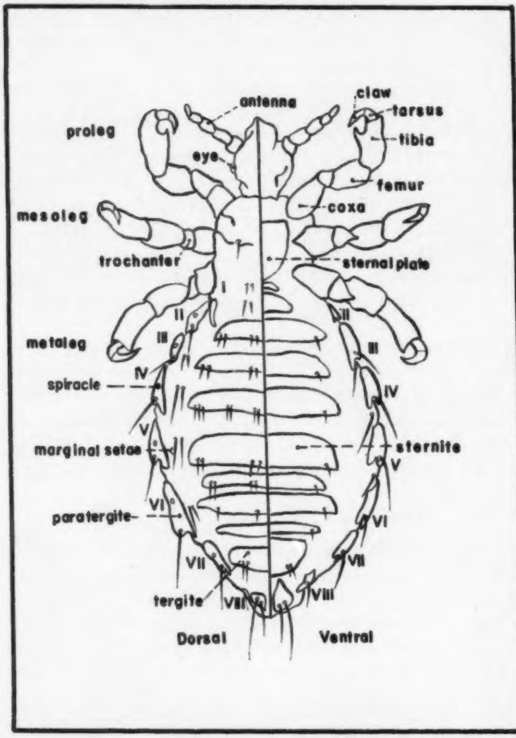

PLATE I—Figure of a hypothetical louse depicting the major key-characters.

KEY TO THE ANOPLURA OF MINNESOTA

Anoplura: small, flat, wingless ectoparasites living in the hair and feeding on the blood of mammals; eggs attached to the host hairs. Head distinct, mouthparts anterior and adapted for sucking blood; antennae normally five-segmented but may superficially appear three- or four-segmented; legs stout, adapted for grasping; tarsus one-segmented, but may appear two-segmented; one tarsal claw. Male: genitalia spoon-shaped, tip of abdomen ending in a point (II-1). Female: genitalia plate-like, tip of abdomen truncate (II-2).

1. Genitalia absent, abdominal paratergites and tergites reduced or absent, setae seldom more than six per segment................nymphs
Genitalia present (II-1, 2) abdominal paratergites and tergites present, setae generally more than six per segment............adults 2

2. (1) Abdomen with paratergal plates (II-3, 4; III-27, 28; IV-4, 5, 6, 7, 16, 17, 18, 19); reduced in *Haemodipsus* (III-8)........................ 3
Abdomen without paratergal plates (II-5, 6)..................................
....(LINOGNATHIDAE) 5

3. (2) Eyes or post-antennal-ocular notch present (II-7, 8); occurs on man and domestic animals... 4
Eyes absent; post-antennal-ocular notch absent (II-9); occurs on rodents and lagomorphs...........................(HOPLOPLEURIDAE) 11

4. (3) Post-antennal-ocular notch present (II-8); head longer than wide; occurs on domestic animals. (HAEMATOPINIDAE)......
....*Haematopinus* 32
Post-antennal-ocular notch absent (II-7, 9); head length equal to width; occurs on humans...............................(PEDICULIDAE) 34

5. (2) Sternal plate of the thorax absent or inconspicuously present as a narrow plate (II-26); occurs on sheep, goat and canids..........
....*Linognathus* 6
Sternal plate of the thorax shield shape (II-27, 28); occurs on domestic cattle and deer...*Solenopotes* 10

6. (5) Sternal plate of the thorax absent... 7
Sternal plate of the thorax present as narrow strip (II-26)........ 9

7. (6) Head less than 2 times as long as wide (II-25); abdominal tergites heavily covered with setae (II-5); occurs on sheep and canids 8
Head 2 times as long as wide (II-24); abdominal tergites not heavily covered with setae; occurs on cattle......*L. vituli* (Linnaeus)*

8. (7) Anterior margin of head rounded (II-17); setae on abdominal tergites not arranged in rows (II-10); occurs on domestic dog, wolf, and coyote...*L. setosus* (von Olfers)*
Anterior margin of head pointed (II-16); setae on abdominal tergites arranged in rows (II-11); occurs on domestic sheep......
....*L. pedalis* (Osborn)*

9. (6) Basal region of head swollen (II-14); occurs on goats and sheep .... *L. africanus* Kellogg and Ferris
Basal portion of head not swollen (II-15); occurs on domestic goats.. *L. stenopsis* (Burmeister)

10. (5) Sternal plate of the thorax a hexagon (II-28); latero-distal margin of head converging medially (II-12); occurs on cattle.......... .... *S. capillatus* Enderlein
Sternal plate of the thorax not hexagonal (II-27); latero-distal margin of head not as above (II-13); occurs on deer................ .... *S. ferrisi* (Fahrenholz)

11. (3) Proleg and mesoleg of same size and form (II-29); occurs on Sciuridae 13
Proleg and mesoleg not the same size and form (II-30)............... 12

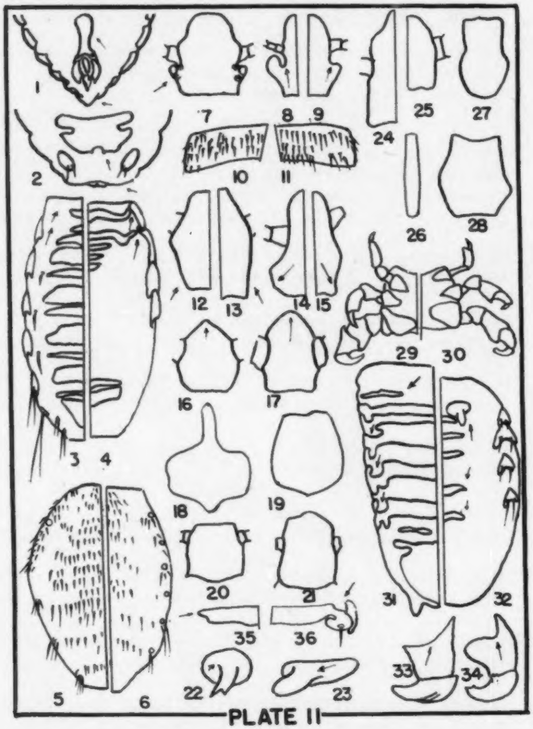

PLATE II

PLATE II (Figs. 1-36)—Key-characters which are used to determine species of *Enderleinellus, Linognathus, Microphthirus* and *Solenopotes* (see key for further explanation).

12. (11) First and second abdominal sternite articulating with paratergite (II-4) 17
First and second abdominal sternite not articulating with paratergite (II-3) 23

13. (11) Second abdominal sternite with a posterior projecting process (II-32); anterior aspects of abdominal sternites not modified into hook process (II-35)........*Enderleinellus* 14
Second abdominal sternite not as above (II-31); anterior aspects of abdominal sternite modified into hook process (II-35); occurs on flying squirrels........*Microphthirus uncinatus* (Ferris)*

14. (13) Sternal plate of the thorax spatulate shape (II-18); basal plate of 2nd abdominal sternite round, process origin in the center of the plate (II-22)........ 15

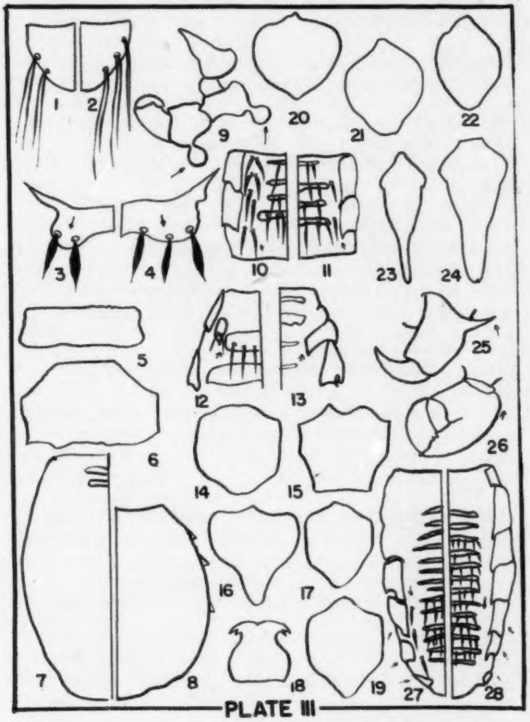

PLATE III (Figs. 1-28)—Key-characters which are used to determine species of *Enderleinellus, Eulinognathus, Fahrenholzia, Haematopinoides, Haemodipsus, Hoplopleura* and *Polyplax* (see key for further explanation).

Sternal plate of the thorax not spatulate shape (II-19); basal plate of 2nd abdominal sternite oval, process origin at one end of the plate (II-23) 16

15. (14) Posterior margin of meta-tarsal segment not emarginate (II-33); length of head equal to width (II-20); occurs on northern red squirrel .... *E. nitzschi* Fahrenholz
Posterior margin of meta-tarsal segment emarginate (II-34); head longer than wide (II-21); occurs on western fox squirrel and northern gray squirrel........ *E. longiceps* Kellogg and Ferris

16. (14) Abdominal segments VI, VII, VIII each with a pair of long setae (III-2); occurs on marmots........ *E. marmotae* Ferris
Abdominal segments VII and VIII each with a pair of long setae (III-1); occurs on *Citellus*........ *E. suturalis* (Osborn)*

17. (12) Antennae with 4 segments (superficially 3-segments); metaleg with balloon structures (III-9); occurs on moles........ *Haematopinoides squamosus* (Osborn)*
Antennae 5-segmented; metaleg not as described above; occurs on squirrels, chipmunks, rats and mice........ *Hoplopleura* 18

18. (17) Sternal plate of the thorax shield or heart-shaped (III-20,21,22); occurs on squirrels and chipmunks........ 21
Sternal plate of the thorax sagitate (III-23,24); occurs on rats and mice 19

19. (18) Setae in margin between abdominal tergites and paratergites; paratergite VI normal, paratergites VII and VIII reduced (III-27) 20
Setae not as described above; paratergites VI and VII normal, paratergite VIII reduced (III-28); occurs on grasshopper mouse, harvest mouse, and deer mouse........ *H. hesperomydis* (Osborn)*

20. (19) Dorsal margin between abdominal and paratergite with one row of setae (III-11); occurs on rats........ *H. oenomydis* Ferris
Dorsal margin between abdominal tergites and paratergites with two longitudinal rows of setae (III-10); occurs on grasshopper mouse, lemming mouse, house mouse, red-backed mouse, and meadow mouse........ *H. acanthopus* (Burmeister)*

21. (18) Posterior projection of 3rd abdominal sternite with three heavy setae (III-4); occurs on flying squirrels........ *H. trispinosa* Kellogg and Ferris*
Posterior projection of 3rd abdominal sternite with two heavy setae (III-3); occurs on squirrels and chipmunks........ 22

22. (21) Sternite of the thorax rounded-triangle shape (III-20); occurs on chipmunks........ *H. erratica-H. aboricola complex** [2]
Sternite of the thorax oval shape (III-22); occurs on tree squirrels .... *H. sciuricola* (Ferris)*

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[2] I was unable to differentiate whether lice collected from *Tamias striatus* (Linn.) and *Eutamias minimus* (Bachman) were *H. erratica* (Osborn) or *H. arboricola* K. & F. These lice did not fit either description, but appeared to fit somewhere in between both species.

23. (12) Abdominal tergites present (IV-4, 5); reduced in females of *Neohaematopinus laeviusculus* (III-7) 27
Abdominal tergites absent (III-8) 24

24. (23) Sternal plate of the thorax absent; head with lateral dentations (III-18); occurs on rats.......... *Eulinognathus* (IV-6) *denticulatus* .... (Cummings)
Sternal plate of the thorax present; head not as described above; occurs on rabbits and mice.......... 25

25. (24) Sternal plate of the thorax oval-shield shape (III-14); meso-tarsi and meta-tarsi projected into point at outer angle (III-25); occurs on pocket mice...... *Fahrenholzia* (IV-7) *pinnata* Kellogg .... and Ferris*
Sternal plate of the thorax box-shape (III-5, 6); meso-tarsi and meta-tarsi not as described above (III-26); occurs on wild and domestic rabits.......... *Haemodipsus* 26

26. (25) Sternal plate of the thorax a rectangle (III-5); occurs on domestic rabbits .... *H. ventricosus* (Denny)
Sternal plate of the thorax a hexagon (III-6); occurs on wild rabbits and hares.......... *H. setoni* Ewing

27. (23) Second abdominal paratergite divided into two plates (III-12); thoracic sternal plate not emarginate posteriorly (II-15, 16, 17, 19), without a posterior projecting process; occurs on rats and mice .... *Polyplax* 28
Second abdominal paratergite not divided into two plates (III-13); thoracic sternal plate posteriorly emarginate (IV-1, 3), or with a posterior projecting process (IV-2); occurs on squirrels and chipmunks.......... *Neohaematopinus* 30

28. (27) Posterior margin of sternal plate of the thorax truncate (III-15); occurs on grasshopper mouse and deer mouse.......... *P. auricularis* .... Kellogg and Ferris
Posterior margin of sternal plate of the thorax convex (III-16, 17, 19); occurs on mice and rats of subfamily Murinae.......... 29

29. (28) Thoracic sternal plate shield shape (III-17, 19); occurs on black, white and house rat, and on meadow mouse.......... .... *P. abscisa-P. spinulosa* complex [3]
occurs on *Microtus* spp. .... *P. abscisa* Fahrenholz
occurs on *Rattus* spp. .... *P. spinulosa* (Burmeister)*

Thoracic sternal plate triangle shape (III-16); occurs on the laboratory mouse and the house mouse.......... *P. serrata* (Burmeister)*

30. (27) Paratergal plates of the abdomen normal (IV-15); Posterior margin of the thoracic sternal plate concave (IV-1, 3); occurs on tree and flying squirrels.......... 31

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[3] The females of this complex could not be differentiated on the basis of structural characteristics. However, the genitalia of the male could be used with a certain degree of reliability as a basis for determination. At present the host species apparently is the best criteria to separate individuals of this complex.

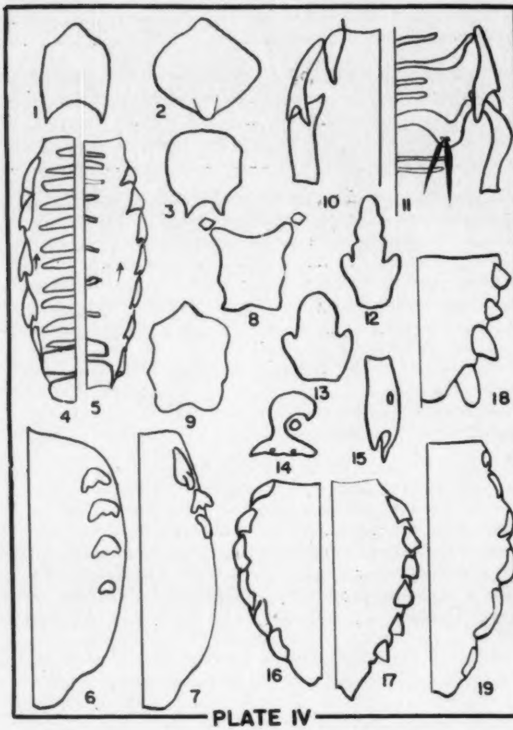

PLATE IV (Figs. 1-19)—Key-characters which are used to determine species of *Eulinognathus, Fahrenholzia, Haematopinus, Neohaematopinus, Pediculus* and *Pthirus* (see key for further explanation).

Paratergal plates of the abdomen reduced; hook-shaped (IV-14); posterior margin of the thoracic sternal plate convex (IV-2); occurs on Richardson's, Franklin's and Thirteen-lined ground squirrels .... *N. laeviusculus* (Grube)*

31. (30) Distance between abdominal paratergites and tergites not greater than length of widest tergite (IV-4); anterior margin of the sternal plate of the thorax rounded (IV-3); occurs on northern and southern flying squirrels.................................. *N. sciuropteri* (Osborn)*
Distance between abdominal paratergites and tergites greater than the length of widest tergite (IV-5); anterior margin of the sternal plate of the thorax convex (IV-1); occurs on western fox and gray squirrels.. *N. sciurinus* (Mjöberg)

32. (4) Abdominal paratergites tubercle-like (IV-17) 33
Abdominal paratergites plate-like (IV-16); occurs on domestic pigs .... *H. suis* (Linnaeus)*

33. (32) Head broad: distance from ocular notch to tip of head equal to distance from ocular notch to base of head (IV-13); anterior margin of thoracic sternal plate convex (IV-9); occurs on cattle .... *H. eurysternus* (Nitzsch)*
Head slender: distance from ocular notch to tip of head greater than distance from ocular notch to base of head (IV-12); anterior margin of thoracic sternal plate concave (IV-8); occurs on the horse and donkey .... *H. asini* (Linnaeus)*

34. (4) Abdominal tubercles absent (IV-19); legs equal in size; body slender; occurs on man .... *Pediculus humanus* (Linnaeus)*
Abdominal tubercles present (IV-18); legs not equal in size; body broad; occurs on man .... *Pthirus pubis* (Linnaeus)*

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References

FERRIS, G. F. 1916.—A catalogue and host list of the Anoplura. Proc. Calif. Acad. Sci. Ser. (Ser. 4) **6**:129-213.

——— 1919-1935.—Contributions toward a monograph of the sucking lice. Stanford Univ. Pub., Univ. Ser., Biol. Sci. **2** (8 parts) 1-634.

——— 1951.—The Sucking Lice. Mem. Pacific Coast Ent. Soc. **1**:1-320.

——— 1953.—Illustrations of three species of sucking lice, with notes on a fourth species (Insecta; Anoplura). Micro-Entomology **18**(2):52-57.

GUNDERSON, H. L. AND JAMES R. BEER 1953.—The Mammals of Minnesota. Univ. of Minn. Press, Minneapolis. 190 pp.

HOPKINS, G. H. E. 1949.—Host associations of the lice of mammals. Proc. Zool. Soc. London **119**:387-604.

KELLOGG, V. L. AND G. F. FERRIS 1915.—Anoplura and Mallophaga of North American mammals. Stanford Univ. Pub., Univ. Ser. 74 pp.

A Study of Yellow Birch (Betula lutea) in the Bogs of Itasca Park, Minnesota[1]

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The occurrence of an organism along the margins of its range of distribution often affords interesting contrasts to its status in the central portion of its range. The present study, which was carried out during the summer of 1957 on three small stands of yellow birch (*Betula lutea*) near the Lake Itasca Forestry and Biological Station, provides data indicating a highly circumscribed habitat in vivid contrast to occurrence within its main area of distribution. In addition to this, the age distribution of the stands, which appears to be the result of pressures from herbivores, is discussed.

The normal habitat of yellow birch is commonly referred to as rich woods (Fernald, 1950) or moist woods (Gleason, 1952). Thus, Potzger (1946), after finding this species in the upland woods of northern Wisconsin, assumed it to be an element of the upland forest in Minnesota as well. However, Rosendahl (1955) clearly states that it is associated with black ash (*Fraxinus nigra*) and tamarack (*Larix laricina*) in boggy situations in Minnesota. Elsewhere at the margin of its range, yellow birch has been found to occur only in bogs (Watts, 1957).

Methods and Results

CHARACTERISTICS OF THE YELLOW BIRCH STANDS

The three stands occur in bogs lying along the shores of Lake Itasca, which is located on a terminal morraine with an irregular topography. The vegetation types in the area can be described as forming a mosaic of forest communities on rolling hills, numerous lakes, and many small marshes and bogs. Kell (1938) points out that the lake lies in a transition zone between the subarctic fir-spruce-birch regions to the northeast, and the deciduous forests and prairies to the south and west. The stands are at Bear Paw Point (NE ¼ Sec. 11, T143 N R 36 W), Roberts Nature Trail (NE ¼ Sec. 11, T143 N R 36 W) and Garrison Point (SW ¼ Sec. 15, T143 R 36 W) — all in Clearwater County, Minnesota. Here yellow birch is at or very near its western limit of distribution.

Once yellow birch were located in the three bogs, the limits of the stands were determined by reconnaissance. As a relatively few trees were found, it was decided to examine each individual over one

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[1] Carried out while the author was the recipient of a National Science Foundation grant-in-aid for research and training at the Lake Itasca Forestry and Biological Station of the University of Minnesota. The author is indebted to Drs. Murray F. Buell and William H. Marshall for their suggestions.

foot in height in considerable detail. Breast-high diameters (DBH) were taken with a diameter tape of all trees over four inches and an Abney level was used to determine heights. Six of the larger trees were checked for age with an increment borer. The general condition of each tree was observed and signs of disease or attack by animals recorded. Individuals under four inches DBH but over one foot in height were counted and recorded as saplings.

The cover and occurrence of associated trees were recorded on a ten-meter line extending through the long axis of each stand. The shrub layer was determined by the line intercept method developed by Bauer (1943). In addition to this the herb cover was studied by sampling on ½ x 2 meter quadrats along the intercept line. Finally the substratum was examined by digging in typical sites.

Twenty-one yellow birch trees with a diameter of over 4 inches were located. Their diameters ranged from 4.1 to 22.8 inches with an average of 9.8 inches. The heights varied from 14.0 to 40.0 feet with an average of 28.2 feet. Few of them reached the top of the forest canopy and those which did exhibited dead or stunted tops. The ages, heights, and DBH of six trees were as follows — 157 rings, 38.5 feet and 22.7 inches; 159 rings, 31.0 feet, and 22.5 inches; 84 rings, 18.3 feet and 13.9 inches; 86 rings, 32.0 feet, and 13.1 inches; 68 rings, 30.0 feet and 7.0 inches; 47 rings, 14.0 feet and 4.1 inches. Only seven trees had healthy tops; nine were classed as stunted, while five had dead crowns. Fourteen grew in water-filled depressions and seven were on hummocks in moist situations. Three of the larger trees exhibited basal scars made by beaver (*Castor canadensis*).

Only one tree with a diameter at breast height of three inches and a height of 13.8 feet was found to be in the sapling class.

There were 380 individuals classed as seedlings on the basis of a diameter of less than one inch and a height of over one foot. Of these, 157 were between 6 and 9 feet tall and 223 were from one to 6 feet tall. Some of these seedlings showed evidence of recent browsing by the snowshoe hare (*Lepus americanus*).

Poorly rooted seedlings of less than one foot in height were numerous and confined to hummocks and decomposed logs projecting above the many water-filled depressions within the bogs.

In summary then, there were twenty-one trees over 4 inches DBH a majority of which did not reach the top of the general canopy. Many showed poor crown condition and a few showed damage by beaver. There was but one sapling between one and 4 inches DBH, and 380 seedlings over one foot in height. Numerous seedlings less than this height occurred. The probable reason for this size distribution will be discussed later.

OTHER PLANTS IN THE AREA

The occurrence of associated tree species as estimated is shown in TABLE I. Clearly, black ash is the most abundant while either balsam

TABLE I.—Species composition of the canopy in three bogs at Itasca State Park

Stand A	%	Stand B	%	Stand C	%
Fraxinus nigra	64	*Fraxinus nigra*	45	*Fraxinus nigra*	61
Abies balsamea	13	*Picea mariana*	16	*Abies balsamea*	22
Betula lutea	9	*Abies balsamea*	15	*Betula lutea*	12
Picea glauca	6	*Betula lutea*	10	*Ulmus americana*	4
Betula papyrifera	3	*Larix laricina*	10	*Populus tremuloides*	1
Ulmus americana	3	*Tilia americana*	3		
Picea mariana	2	*Ulmus americana*	1		

fir (*Abies balsamea*) or black spruce (*Picea mariana*) is of secondary importance. The six other species were of minor importance in each stand.

The mountain maple (*Acer spicatum*) made up a major portion of the shrub layer in all three bogs (Table II). Six other species, all commonly attributed to wet situations, occurred in the area in appreciable percentages.

The herb cover varied in composition within each stand because of the uneven terrain. The abundant herbs of the larger wetter depressions were marsh marigold (*Caltha palustris*) and the cat-tail (*Typha latifolia*). Manna grass (*Glyceria striata*) and *Carex* of several species, especially *C. lasiocarpa* and *C. leptalea,* were found in all three bogs. Several species of Ericaceae were abundant on the hummocks which were largely composed of the mosses *Mnium* and *Sphagnum.* Eighteen other herbs, mostly of aquatic affinities, were found.

These records of associated plants clearly show the very wet nature of the restricted habitats in which yellow birch is found in Itasca Park.

RELATION OF AGE OF TREES TO ANIMAL NUMBERS

On review of the size classes of yellow birch in the three stands it becomes apparent that there are a few trees over four inches in diameter and about 50 years of age, only one sapling of 3 inches DBH and

TABLE II.—Estimate of shrub cover based on a line intercept count in three bogs at Itasca State Park

Stand A	%	Stand B	%	Stand C	%
Acer spicatum	38	*Acer spicatum*	42	*Acer spicatum*	52
Betula pumila	15	*Alnus rugosa*	20	*Alnus rugosa*	15
Alnus rugosa	14	*Betula pumila*	15	*Betula pumila*	11
Cornus stolonifera	13	*Cornus stolonifera*	15	*Rhamnus alnifolia*	10
Salix candida	12	*Salix candida*	6	*Cornus stolonifera*	5
Rubus pubescens	5	Others	2	*Rubus spp.*	3
Others	3			*Salix candida*	3
				Others	1

many seedlings up to 9 feet tall. It is thought, on the basis of the following data, that the lack of saplings may be attributed to the history of beaver and white tail deer (*Odocoileus virginianus*) populations in the park.

Bailey (1927) discusses beaver populations in Itasca Park between 1900 and 1921. While beaver were scarce or absent about 1900, three, a male and two females, were released in the park in 1901. By 1916 a count showed 127 used houses with an estimated population of at least 635 and very possibly more. Apparently severe damage was done to trees along the lake shore by this time, and although the park was a game refuge, controlled trapping was initiated in 1917. The beaver population continued to increase and in 1921 it was estimated at over 1000 animals.

Unpublished reports by W. S. Feeney, who was stationed in the park as a wildlife technician in the early 1930's, are of great interest. In the summer of 1934 at least 123 active lodges were located within the boundaries of Itasca Park. These beaver were primarily dependent on alder (*Alder rugosa*) and there was literally no aspen (*Populus tremuloides*) available near any water in the park. Pictures submitted with these reports clearly show that beaver populations were nearly wiped out by the combination of the drought of 1934 and the very severe winter of 1934-35.

Thus certainly between 1920 and 1935 very severe pressures were exerted by beaver against all hardwood trees that were close to water. The three stands studied were in close proximity to Lake Itasca.

Unpublished notes of W. H. Marshall on the history of the white tail deer reveal another span of heavy pressures by this animal against hardwoods in the area from about 1930 to 1945. Population estimates, based on a drive by CCC crews, reached 75 animals per square mile by 1939 (Fredine, 1940). Old pictures of that period indicate extremely heavy deer browsing throughout the park. In 1936 a field report by G. M. Amidon states that at least 500 deer died of starvation in the park. These losses ranged to an estimated 1000 deer by 1940 according to Fredine (*op. cit.*). A nearly complete elimination of the deer herd was brought about by hunting in November of 1945, when some 2300 deer were known to have been removed from the park.

From these data it can be surmised that deer exerted extreme pressures against small hardwoods, particularly in bogs, for another ten years after the beaver population had died off. Thus for approximately thirty years starting in 1915, yellow birch in bogs adjacent to water areas were undoubtedly browsed and/or eaten by these two herbivores to an extreme. The fact that only one yellow birch sapling was found and that the youngest tree was 47 years old in 1957 appears to be correlated with this history of animal populations. The numerous seedlings had probably become established after 1945.

SUMMARY

Three isolated stands of yellow birch containing twenty-one trees, one sapling, and 380 seedlings over one foot in height were located in bogs near Lake Itasca in northwestern Minnesota.

Associated tree, shrub and herb species clearly indicate the very moist nature of the boggy habitat to which the yellow birch is restricted in the Itasca Park area. Its absence on upland sites is in contrast to what is found throughout the main parts of its range.

The age distribution of yellow birch appears to be a result of the heavy pressures from beaver and white tail deer during the period 1916 to 1945.

REFERENCES

BAILEY, V. 1927—Beaver habits and experiments in beaver culture. U.S.D.A. Tech. Bull. **21**:1-40.

BAUER, H. L. 1943—The statistical analysis of chaparral and other plant communities by means of transect samples. Ecology **24**:45-60.

FERNALD, M. L. 1950—Gray's manual of botany (8th Ed.) New York, American Book Co. 533 pp.

FREDINE, GORDON 1940—A census of deer populations in Itasca Park. Unpublished.

GLEASON, H. A. 1952—Illustrated flora of the northeastern United States and adjacent Canada. New York, New York Botanical Garden.

KELL, L. L. 1938—The effect of moisture-retaining capacity of soils on forest succession in Itasca Park, Minnesota. Amer. Midl. Nat. **20**:682-694.

POTZGER, J. E. 1946—Phytosociology of primeval forests in northern Wisconsin and Upper Michigan, and a brief post-glacial history of the lake forest formation. Ecol. Monogr. **16**:211-250.

ROSENDAHL, C. O. 1955—Trees and shrubs of the upper midwest. Minneapolis, University of Minnesota Press. 104 pp.

WATTS, M. T. 1957—Reading the landscape. New York, The Macmillan Co. 230 pp.

Notes on the Ecology of Slugs: Arion circumscriptus, Deroceras reticulatum, and D. laeve

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Information concerning the ecology of slugs is rather limited, particularly that of North American forms. A few European papers have treated species that also occur in North America (Barnes and Weil, 1944, 1945; Dainton, 1954). The few papers from North America have dealt primarily with the economic aspeets of slugs (Lovett and Black, 1920; Karlin and Naegele, 1958) or with some particular phase of their biology such as feeding habits (Ingram and Peterson, 1947).

In the course of field studies of a small mammal population near Ann Arbor, Michigan, three species of slugs, *Arion circumscriptus* Johnson, *Deroceras reticulatum* (Muller), and *D. laeve* (Muller) were found together. Two of these forms (*A. circumscriptus* and *D. reticulatum*) have been introduced from Europe, while *D. laeve* is native to North America. *D. reticulatum* is now well established as one of the more abundant slugs in North America. *A. circumscriptus* is recorded in many localities from New York to California (Pilsbry, 1948). Its distribution is quite local, however, and it is found apparently only around areas of human habitation (or from near refuse dumps, campsites, and the like).

D. reticulatum and *A. circumscriptus* are unrelated, but native to the same region; *D. reticulatum* and *D. laeve* are closely related, but originated in different regions. This relationship seemed to present an ideal situation for a comparative study of some aspects of their ecology. Of special interest is the relative importance of taxonomic affinity and region of origin as related to some of the ecological factors. A number of field observations were obtained which seemed to indicate several differences in their ecology. Laboratory experiments were then designed to test the validity of these observations.

The studies reported here are preliminary. The experiments were simple and less comprehensive than desirable, but for the most part they give the desired data and a few general conclusions can be drawn from them. More intensive investigations in both field and laboratory are needed to determine the significance of some of the results.

Differences in activity patterns (seasonal as well as responses to shorter weather variations) and habitat preferences were observed. The ecological factors which appeared most important in explaining some of these observations were temperature, moisture, and food preferences. Experiments were conducted to determine the importance of these factors.

A few experiments were also conducted to investigate toleration of

extremes. Numerous factors such as physical condition, age, prior acclimation, length of time the stress is applied, and interrelation of stress factors (i.e. humidity variations with temperature extremes) can influence tolerance. Hence it is quite difficult to determine experimentally, the conditions under which the animal might survive in the field. These experiments were therefore only exploratory in nature.

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Description of the Study Area

All field work was conducted in the University of Michigan's Mud Lake Area, located in sections 1 and 12 of Webster Township, Washtenaw County, Michigan. The main area which the slugs cohabited was an abandoned field (last cultivated approximately 15 years ago). The vegetation consisted primarily of *Poa compressa.* Other abundant plants included *Potentilla intermedia, Daucus Carota, Taraxacum officinale* and *Barbarea vulgaris.* The surface was covered by a moss, *Brachythecium* sp. The soil was a sandy loam.

An adjacent area was also studied. This was a pasture which likewise had been abandoned for several years. The vegetation here consisted primarily of a dense stand of *Poa pratensis* with a few scattered second growth *Quercus, Carya,* and *Corylus* sprouts. A leaf mold was developed under the trees. There were also numerous boards lying on the ground as well as several refuse heaps (tin cans, garbage, etc.). Other nearby habitats were briefly investigated; they will be discussed where pertinent.

Estimates of the relative number of slugs in the various habitats were obtained incidental to the other field work. These data were obtained by counting slugs congregating under the traps utilized in the mammal study, from studies of the soil invertebrates and from general observations. While such information does not give precise comparative population densities, it is possible to gain a fairly accurate estimate of the relative abundance of slugs in the various habitats. The period of study was from April, 1957, through September, 1958.

Habitat Preferences

Arion circumscriptus.—This species occurred only in the two areas described above and in a variety of situations within these habitats. Almost without exception, the slugs were found more or less secluded under some object or below the vegetation. Only during the night, or on overcast, rainy days, were they active on the surface and then only rarely. Some of the specific situations in which *A. circumscriptus* has been observed are as follows: under logs and boards, under the bark

of decaying logs, under the leaf mold, in the humus at the edge of a sedge marsh (but not in the marsh itself), under metal and other debris in the rubbish piles, at the bases of *Poa pratensis* plants, and under the moss in the old field. This species of slug has evidently been in the area for some time (as indicated by a high population density), but has not succeeded in colonizing a sedge marsh or hardwood swamp adjoining the area. Observations indicated no significant differences in the population densities in the field or pasture.

Deroceras reticulatum.—This species was found in essentially the same habitats as *A. circumscriptus.* It was not as secretive as the latter species and appeared in the open even during the clear days. It seemed to avoid the edge of the sedge marsh and was seldom found under the bark of decaying logs. In contrast to *A. circumscriptus, D. reticulatum* appeared to be slightly more abundant in the old field than in the pasture.

Deroceras laeve.—This species occurred in a greater variety of situations than either *A. circumscriptus* or *D. reticulatum.* In the immediate vicinity of the study area it was observed in the same situations as *A. circumscriptus* and *D. reticulatum.* In addition, it was observed in the following habitats: a hardwood swamp, a *Sphagnum* bog, an oak hickory upland and a sedge marsh. It was most abundant in the

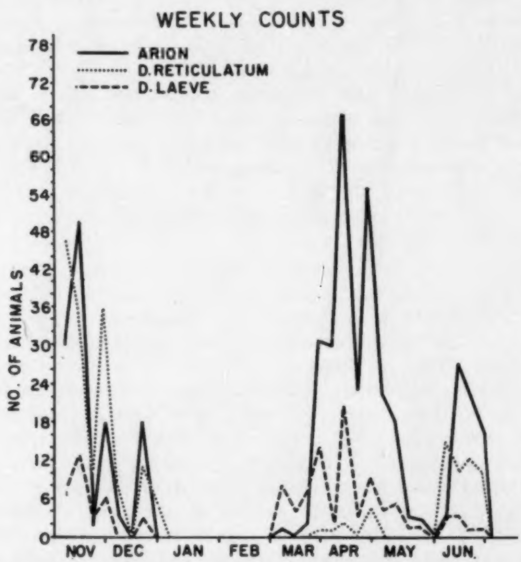

Fig. 1.—Weekly counts of slugs occurring under boards in an abandoned pasture.

sedge marsh; the next highest population density occurred in the old field.

ACTIVITY PATTERNS

As used here, activity refers to the presence of the slugs on the surface of the soil, under such objects as logs, boards, leaf mold, etc., or actively crawling on the vegetation. The alternate condition is when they are below the surface of the soil (i.e. either aestivating or hibernating).

In order to determine the seasonal activity of the three species, weekly counts were made of the slugs occurring on or under the boards in the pasture habitat. The same boards were checked each week. The counts were made from November 7, 1957 through June 27, 1958. The summer was quite dry and resulted in the drying of the soil under the boards. No slugs occurred under the boards after the soil dried out. The number of slugs of each species present are used as an index to relative periods of entry into an inactive state and emergence from such a state (Fig. 1).

In the spring *D. laeve* became active approximately three weeks before *A. circumscriptus* and *D. reticulatum*. In the winter, all went into hibernation at approximately the same time. During the rest of the year, large fluctuations occurred which appeared to be related to changes in soil moisture and possibly temperature. From the experimental data, it will be seen that *D. laeve* is more tolerant of low temperatures than either *A. circumscriptus* or *D. reticulatum*. This quite possibly accounts for its early appearance. Even though all species entered into hibernation at approximately the same time, there was a considerable increase in numbers of *D. laeve* in the old field in November (approximately 15 times more abundant the first week of November, 1957, than the first week of September or October of 1957). A decrease in abundance occurred in *A. circumscriptus* and *D. reticulatum* at this time.

Adults of both *A. circumscriptus* and *D. laeve* were quite abundant throughout the spring and summer. In the case of *D. reticulatum*, however, a different phenomenon was observed. Only a very few individuals, all adults, appeared in the early spring and no more adults were observed emerging later on. The adults produced eggs almost immediately after emerging. Those individuals observed in June were young produced from these eggs, and almost the entire summer population was presumed to be composed of young of the year. It thus appears that in this area *D. reticulatum* is an annual species with only a few adults surviving the winter to lay eggs in the spring. This phenomenon is common in other species of mollusks (Boycott, 1934; Fromming, 1953). Individuals of *D. laeve* and *A. circumscriptus* apparently live more than one year, since adults, obviously from the preceding year, were quite abundant throughout the spring and early summer. From the size of some of the individuals and the growth

rate of the young as observed in the field, it appears that *A. circumscriptus* lives for at least two or three years.

In order to obtain information concerning factors influencing daily activity of the slugs, counts were made of the slugs occurring on or under the live traps used in the mammal study. Each trap was 6″ x 3″ x 3″ and constructed of ½″ white pine or redwood. The traps were placed in a 40-foot grid pattern covering the old field and remained in the same positions during the entire trapping period (five days). The traps were checked twice a day, approximately one hour after sunrise and one hour before sunset.

During the period of September 7-11, 1957, the first two days were dry and clear as had been the previous two weeks. During the night of the 9th it rained (1 cm), and the remaining days and nights were

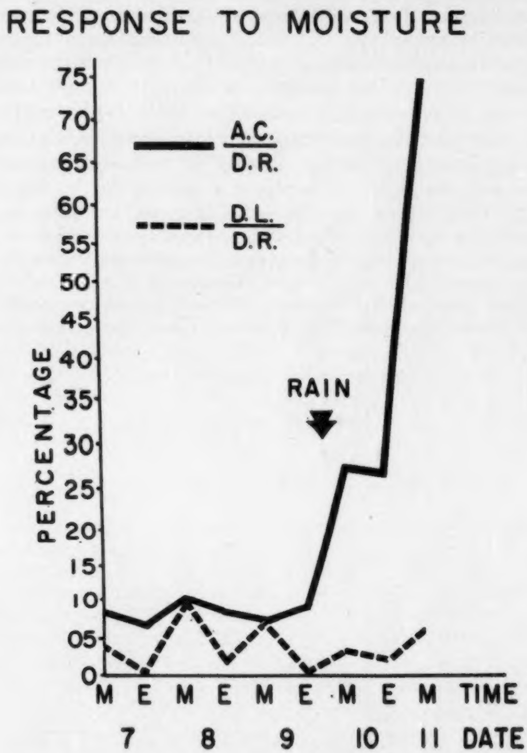

Fig. 2.—Comparison of the relative abundance of active slugs before and after a rain. M—one hour after sunrise; E—one hour before sunset; A.C.—*A. circumscriptus;* D.R.—*D. reticulatum;* D.L.—*D. laeve.*

cloudy. After the rain there was an increase in the number of both *A. circumscriptus* and *D. reticulatum,* while *D. laeve* remained about the same. In relation to the increase of *D. reticulatum,* the increase of *A. circumscriptus* was much greater (Fig. 2). This seems to indicate a greater response to moisture by *A. circumscriptus* than by *D. reticulatum.* No correlation with the temperature data appears. This conclusion is further supported by experimental evidence discussed below.

Moisture Requirements

Field observations indicated that *A. circumscriptus* required a more moist situation for activity than did *D. laeve* or *D. reticulatum.* They also revealed that *D. laeve* was abundant in wet situations (i.e. marshy and swampy areas). Therefore, it seemed desirable to obtain some experimental data concerning the moisture preferences of the three species. Neither time nor funds were available to construct a device for obtaining a humidity gradient. A substrate moisture gradient was used instead. This consisted of ten pads, 2″ x 1″, (made of six thicknesses of paper toweling) placed in a 24″ x 1″ copper trough (the same one used in the temperature gradient experiments to be described later) with a space of about 1/3″ between each pad. Starting at one end, five drops of water were placed on the first pad with an increase of five drops on each succeeding pad so that a gradient of five through fifty was established. The humidity conditions were probably the same throughout the box, but the substrate varied from quite dry to saturation.

Two slugs were placed on each pad and an acetate covering positioned ⅜″ above the floor. The entire box was covered to exclude all

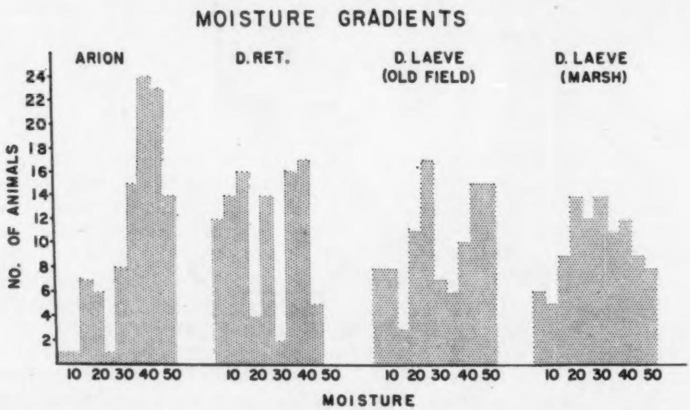

Fig. 3.—Reaction to substrate moisture gradients. The larger numbers indicate higher moisture contents.

light and the box placed so that a temperature gradient was not present (the experiments were conducted at room temperature, 18° to 20°C). Experimentation showed that both *D. reticulatum* and *D. laeve* became oriented after two or three hours but that *A. circumscriptus* required more time. Each trial was, therefore, allowed to remain undisturbed for 24 hours. At this time a count was made of the slugs occurring on each pad.

Five trials (a total of 100 animals) were made with each species. The results (Fig. 3) show rather conclusively that *A. circumscriptus* favors a more moist substrate than either *D. reticulatum* or *D. laeve*. The latter two do not appear to select any particular position in the moisture gradient. A comparison was also obtained between individuals of *D. laeve* from the old field and the sedge marsh. There is no significant difference in their moisture preferences, although extreme differences exist in the substrate moisture of the two habitats.

Desiccation and toleration to drowning experiments were conducted on all three species. The desiccation experiments involved the use of petri dishes with pieces of dry filter paper in the bottom serving as desiccating agents. One individual of each species was placed in a petri dish. The dishes were then periodically observed to determine the length of time each could survive. In all, twelve such experiments were completed. There was considerable variation in the length of time the animals survived (as a result of the variables mentioned previously). In all cases, however, both *D. reticulatum* and *D. laeve* survived considerably longer (2-12 hours) than *A. circumscriptus*. No differences were noted between *D. reticulatum* and *D. laeve*.

The drowning experiments consisted of placing one individual of each species in a small vial filled with well water. The vial was corked so that no air bubbles were present. Observations were then made to determine the length of survival. Six such experiments were conducted. No differences were noted between the species. Survival time was at least four hours in all cases.

TEMPERATURE PREFERENCES

The method used to obtain a suitable temperature gradient was similar to that of Dainton (1954). A box was constructed of 1/16″ sheet copper lined with tin on the inner side. The inside dimensions (the experimental area) were 24″ x 1″ x 1″ with a 2″ x 1″ x 1″ watertight compartment at each end. Each compartment was provided with an inlet and outlet tube. An acetate cover held in place by a series of flanges was placed ⅜″ above the floor of the experimental area. This kept the animals on the same plane and avoided vertical temperature gradients. The top was covered by a piece of ¼″ plate glass with holes drilled to permit insertion of thermometers. Nine thermometers, spaced two and one-half inches apart, were placed along the tank; the two terminal ones were located ¾″ from the ends of the tank. The bulbs of the thermometers were placed at the level

of the acetate covering. A strip of blotter material was placed on the bottom of the tank and over this a strip of white paper marked off into 24 one-inch sections. The whole tank was placed in a wooden box packed with cotton.

In conducting the experiment, the blotter material was saturated with water to provide a uniform humidity throughout the tank. The acetate and plate glass covers were then replaced. By running hot water through one end compartment and cold water through the other, a temperature gradient was established along the tank. The water running through the cold end was first routed through a copper

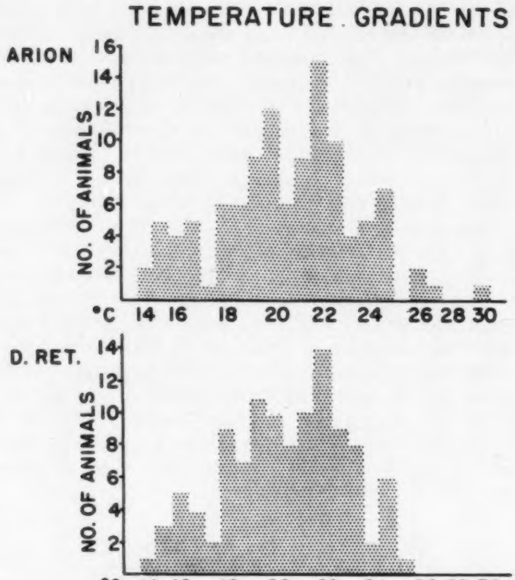

Fig. 4.—Reaction to temperature gradients.

coil in a canister of ice in order to cool it sufficiently. By varying the temperatures of the water, the desired gradient was established.

Once the gradient was established, the slugs were introduced. Twenty-two individuals of the same species were placed in the tank during each trial. One individual was placed in each of the one-inch sections except the two end ones. Trial runs showed that with the gradient used the temperatures in the two end sections were extreme, and often the slugs were killed or immobilized before they could move out. The two covers were replaced and sheets of dark paper were placed over the entire experimental area and the room darkened. This eliminated the possibility of light influencing the result. After 45 minutes (trial runs showed that the slugs had oriented themselves by this time) the number of slugs in each section (the section in which the head was located) was counted and recorded. The results are shown in Figure 4.

These data show that *A. circumscriptus* and *D. reticulatum* both prefer temperatures between 18° to 24°C. *D. laeve,* on the other hand, was much less selective, grouping between 14° to 26°C (and possibly even at a lower temperature).

Experiments were constructed to determine toleration to both low and high temperatures. The cold toleration experiments consisted of placing three individuals of each species in a petri dish (provided with wet filter paper). These dishes were cooled to approximately 10°C for 30 minutes and then subjected to the experimental temperatures. An ordinary refrigerator was used to obtain the desired temperatures. A Taylor maximum-minimum thermometer was utilized to make sure a relatively stable temperature had been maintained.

Several experiments were conducted at different temperatures and lengths of time. The results were somewhat variable. They do show that *D. laeve* is able to survive much lower temperatures than either *A. circumscriptus* or *D. reticulatum.* In one experiment, the animals were subjected to -8° C for five hours. All were frozen solid at the end of the experiment. All individuals of *D. laeve* revived upon being thawed out, while all individuals of the other two species died. A similar experiment at -10° C resulted in the death of all the animals.

In general, it appears that *D. laeve* can tolerate subfreezing temperatures while both *D. reticulatum* and *A. circumscriptus* are killed by them. Two field observations tend to confirm this observation. A jar of animals to be used in experimentation was inadvertently left in the field overnight (October 12, 1957). The temperature dropped below freezing during the night. When checked the next morning, ice crystals had formed in the jar and the animals were all partially frozen. Approximately 60 individuals of each species were in the jar. Of these, all of the *D. laeve* survived while all individuals of the other two species died. On March 5, 1958, several frozen individuals of *D. laeve* were collected from the sedge marsh. When thawed out, these individuals were found to be alive and apparently in good condition.

Toleration to heat was determined by subjecting the animals to

varying temperatures between 33° to 38° C. This was done by placing one individual of each species in a small vial containing a piece of wet filter paper. These vials were then immersed for 15 minutes in water at the desired temperature. From these experiments it appears that both *D. reticulatum* and *D. laeve* can tolerate temperatures up to 36° C, while *A. circumscriptus* is killed by temperatures over 35° C.

One set of observational data tend to support this conclusion. A petri dish containing 15 individuals each of *A. circumscriptus* and *D. reticulatum* was unknowingly left where the sunlight could fall on it. A thermometer lying beside it recorded a maximum temperature of 36° C. When it was later checked, all individuals of *A. circumscriptus* had died, while all *D. reticulatum* survived. Although the differences are slight, it appears that *A. circumscriptus* is less tolerant of high temperatures than either of the other two species.

FEEDING HABITS

Laboratory experiments were conducted to obtain information concerning the feeding habits of the slugs. Leaves of plants to be tested were placed in petri dishes provided with pieces of wet filter paper. Five slugs (of one species) were placed in each dish and left for a period of three days. At the end of this time, a check was made to determine if the food had been accepted. Records were kept as to whether it was rejected, reluctantly eaten, or readily eaten. Forty-five species of common plants occurring in the study area were tested. Such feeding experiments do not give precise data concerning the feeding habits of a species under natural conditions, but they give certain indications.

From the results of these experiments (Table I), it appears that *D. laeve* feeds on a wider variety of plants than either *D. reticulatum* or *A. circumscriptus*. It can further be seen that there is more similarity between the feeding habits of *D. reticulatum* and *A. circumscriptus* than between *D. reticulatum* and *D. laeve*, or between *D. laeve* and *A. circumscriptus*. As *D. laeve* is native to the region, it might be assumed that it would be adapted to the native plants and thus have a more varied feeding habit. However, many of the species of plants involved in the study either have been introduced from Europe or occur in both North America and Europe. It thus appears that *D. laeve* is simply less restricted in its feeding habits.

From limited field observations, it appears quite likely that *A. circumscriptus* feeds to some extent upon decaying leaf mold. Specimens observed in the leaf mold apparently were feeding on the humus. Examination of the feces revealed what appeared to be remnants of such feeding. Feeding of decaying humus in captivity was inconclusive. Fromming (1954) has discussed the feeding habits of *A. circumscriptus*.

TABLE I.—Results of captivity feeding of leaves

Species	*Arion*	*D. reticulatum*	*D. laeve*
Taraxacum officinale	**	**	**
Plantago major	**	**	**
Asclepias sp.	**	**	**
Aster sp.	**	**	**
Aralia nudicalis	**	**	**
Symplocarpus foetidus	**	**	**
Rumex Acetosella	**	**	**
Monarda fistulosa	**	**	**
Cirsium vulgare	**	**	*
Trifolium repens	**	*	*
Barbarea vulgaris	*	*	**
Poa pratensis	*	*	*
Claytonia virginica	*	*	*
Arctium minus	*	**	—
Dipsacus sylvestris	*	*	—
Typha latifolia	*	*	—
Solidago sp.	*	—	**
Osmunda regalis	—	*	**
Melilotus alba	—	*	**
Daucus Carota	—	*	**
Hypericum perforatum	—	*	**
Maianthemum canadense	—	*	*
Poa compressa	—	*	*
Anemonella thalictroides	—	*	—
Plantago lanceolata	—	*	—
Thalictrum dasycarpum	—	*	—
Impatiens capensis	—	*	—
Oenothera biennis	—	—	**
Onoclea sensibilis	—	—	**
Vitis sp.	—	—	**
Rhus radicans	—	—	**
Osmunda cinnamomea	—	—	*
Rumex crispus	—	—	*
Podophyllum peltatum	—	—	*
Caltha palustris	—	—	*
Potentilla recta	—	—	*
Carex sp.	—	—	—
Geranium maculatum	—	—	—
Oxalis sp.	—	—	—
Verbascum Thapsus	—	—	—
Linaria vulgaris	—	—	—
Potentilla intermedia	—	—	—
Fragaria virginiana	—	—	—
Potentilla palustris	—	—	—
Brachythecium sp.	—	—	—

Symbols: ** readily accepted; * reluctantly accepted; — refused.

Reproduction

A few observational notes were obtained on the reproductive habits of the three species. *D. reticulatum* and *D. laeve* begin laying eggs almost as soon as they emerge in the spring. The first eggs observed for *D. reticulatum* were on April 4, 1958, while those of *D. laeve* were first found on March 21, 1958. Egg laying apparently continues throughout their period of activity, as eggs of both species were found in the summer and late fall. One pair of *D. reticulatum* was observed copulating on November 29, 1957. *A. circumscriptus* apparently lays its eggs in late August or early September (eggs were first observed on September 2, 1957), and continues to do so until it enters into hibernation.

As discussed above, *D. reticulatum* is an annual species with only a few individuals surviving the winter. Eggs laid in the spring hatch to form the summer and fall populations. *D. laeve* lives at least one year and *A. circumscriptus* may survive for two or three years.

Discussion

From the above data, it can readily be seen that *D. laeve* is less restricted in its requirements than either *A. circumscriptus* or *D. reticulatum*. Although more abundant in the marsh, *D. laeve* shows no preference for moisture.

Of particular significance is *D. laeve's* toleration of subfreezing temperatures. This apparently permits it to inhabit the marsh. During the winter the marsh is inundated, except for small hummocks of decaying humus around the bases of sedges, 4 to 6 inches above the surface. The slugs must hibernate in these hummocks. If hibernation occurred at a deeper depth, the slugs would be below the water. When they hibernate so near the surface, they are subjected to subfreezing temperatures. Were they not adapted to low temperatures, they probably would not be able to occupy this habitat. The same conclusions may also be true for those portions of the other habitats in which the water level is quite near the surface. Pearl (1901) has indicated that *D. laeve* may hibernate in water, but this has not been confirmed.

A. circumscriptus seems to prefer moist conditions. It has not succeeded in colonizing a hardwood swamp or marsh bordering the study area, so moisture is not the only factor important in its habitat selection. Its sensitivity to freezing temperatures, as suggested above, may be important. However, since *A. circumscriptus* is absent even from the portions of the hardwood swamp which are never inundated, other factors may be involved. The narrow range of temperature preference apparently has no significance in its habitat selection. Temperature data frcm all the habitats show that the old field experiences wider fluctuations than any other habitat (with the possible exception of the bog).

Food preferences do not indicate any limiting factors. Two of

the more abundant species occurring in the hardwood swamp (*Aralia nudicaulis* and *Symplocarpus foetidus*) were readily eaten.

Factors such as soil type and physiognomy of the surface (type of litter, etc.) may be possible limiting factors. Insufficient data concerning these factors were obtained to draw any conclusions.

The data do not offer any explanation for the absence of *D. reticulatum* in all the habitats, except the field and pasture. Its moisture requirements are similar to those of *D. laeve*. Its lack of toleration to freezing temperatures may explain its absence from the marsh and similar habitats. It still does not explain its absence from the drier habitats, such as the oak-hickory upland. The same conclusions concerning temperature and food preferences given for *A. circumscriptus* also apply to *D. reticulatum*.

As *D. laeve* is native to the region, one would expect it to be adapted to a wider variety of habitats. Both *D. reticulatum* and *A. circumscriptus*, as recently introduced species, have probably not had time to become adapted to all the habitats present.

In comparing the ecology of the three species, the importance of region of origin and taxonomic affinities varies with the factor being considered. *D. reticulatum* parallels *A. circumscriptus* in temperature and food preferences as well as in toleration of low temperatures, while it resembles *D. laeve* in its moisture preference and toleration of high temperatures and desiccation. No resemblances occur between *A. circumscriptus* and *D. laeve*. From the species considered in this paper, taxonomic affinities and area of origin seem about equally important in giving rise to ecological similarities.

SUMMARY

Three species of slugs (*Arion circumscriptus, Deroceras reticulatum*, and *D. laeve*) were found occurring together near Ann Arbor, Michigan. *D. laeve* is native to the region, while *A. circumscriptus* and *D. reticulatum* have been introduced from Europe.

A. circumscriptus and *D. reticulatum* were restricted to an abandoned field and pasture. *D. laeve* also occurred in a hardwood swamp, a spruce swamp, a *Sphagnum* bog, an upland hardwood forest, and a sedge marsh.

Field data showed *A. circumscriptus* to be more responsive to increases in substrate moisture than either *D. reticulatum* or *D. laeve*.

D. laeve appeared approximately three weeks earlier in the spring than either *A. circumscriptus* or *D. reticulatum*. All entered into hibernation at approximately the same time in the fall.

Experimental data showed *A. circumscriptus* to select a more moist substrate while *D. reticulatum* and *D. laeve* selected no particular moisture range. *D. reticulatum* and *D. laeve* were more tolerant of desiccation than *A. circumscriptus*. Differences in toleration to drowning were inconclusive.

Experimental data showed *A. circumscriptus* and *D. reticulatum*

to select a more narrow temperature range (18°-24°C) than *D. laeve* (14°-26°C). *D. laeve* was more tolerant of subfreezing temperatures than were *A. circumscriptus* and *D. reticulatum*. *D. reticulatum* and *D. laeve* were slightly more tolerant of high temperatures than *A. circumscriptus*.

D. laeve had a more varied food preference (utilizing 18 of 45 species) than *D. reticulatum* or *A. circumscriptus* (each utilizing 10 of 45 species).

The data do not explain the restriction of *A. circumscriptus* and *D. reticulatum* to two habitats. *D. laeve apparently* is able to inhabit the marsh due to its toleration of subfreezing temperatures.

A. circumscriptus and *D. reticulatum,* unrelated but native of the same region, were similar in regards to three factors: temperature preference, cold toleration, and food variability. *D. reticulatum* and *D. laeve,* closely related but native of different regions, were similar in regards to three factors: substrate moisture preferences, heat toleration, and toleration to desiccation. No similarities between *A. circumscriptus* and *D. laeve,* unrelated and native of different regions, were obtained.

REFERENCES

BARNES, H. F., AND J. W. WEIL 1944—Slugs in gardens: their numbers, activities and distribution. Part I. Jour. Animal Ecol. **13**:140-175.

———1945—Slugs in gardens: their numbers, activities and distribution. Part II. *Ibid.* **14**:71-105.

BOYCOTT, A. E. 1934—The habitats of land mollusca in Britain. Jour. Ecol. **22**:1-38.

DAINTON, B. H. 1954—The activity of slugs. Jour. Exptl. Biol. **31**:165-197.

FROMMING, E. 1954—Biologie der mitteleuropaischen Landgastropoden. Berlin, Duncker and Humbolt. Pp. 1-404.

INGRAM, W. M. AND A. PETERSON 1947—Food of the giant western slug, *Agriolimax columbianus* (Gould). Nautilus **61**:49-51.

KARLIN, E. J., AND J. A. NAEGELE 1958—Slugs and snails in New York greenhouses. Cornell Bull. **1004**:1-5.

LOVETT, A. L. AND A. B. BLACK 1920—The gray garden slug. Oregon Agric. Expt. Sta., Bull. **170**:1-43.

PEARL, R. 1901—A curious habit of the slug, *Agriolimax*. Mich. Acad. Sci. 3rd Rept. Pp. 75-76.

PILSBRY, H. A. 1948—Land Mollusca of North America (North of Mexico). Phil. Acad. Nat. Sci. Monogr. No. **3**. Vol. II, pp. 521-1113.

Moisture Regulation in Mound Nests of the Ant, *Formica ulkei* Emery[1]

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The construction of an earthen mound in which young are hatched and sometimes reared is a widespread habit found not only among the social insects but also in certain birds, alligators, beaver and muskrat. It is a reasonable assumption that not only protection from predators but also a regulated or modified microclimate regime results from this habit. This has, in fact, been satisfactorily demonstrated for the Australian Mallee-Fowl (Lewis, 1940; Firth, 1956) and for termite mounds (Holdaway and Gay, 1948). The situation in ant mounds is less clear, and in this paper an attempt is made to determine if the construction of a mound nest by one species of mound-building ant results in a regulated microclimate with respect to the moisture content of the mound, and if so, whether a relationship exists between the moisture content of the mound and the moisture preferendum of the inhabitants. This specific question is pertinent to the broader ecological problem of how animals cope with the fluctuations in the external physical environment.

Mound nests are, of course, not the only habitats in which the activity of the organism modifies the microclimate of its surroundings. To a limited extent most organisms, simply by their metabolic activity, probably alter their environment. But this ability appears marked only in a few habitats such as the hives of honey bees, the carton nests of certain wasps and the honeycombs of the wax moth *Galleria mellonella* L. (Allee *et al.,* 1949). A unique case is the modified microclimate achieved by certain Army ants of the genus *Eciton* in which the brood shelter, or bivouac, is formed entirely of the linked bodies of living ants (Schneirla, Brown and Brown, 1954).

The microclimate within ant mounds has been measured by a large number of investigators working in several different countries. Most of their papers report data on temperature relationships, while a few deal with the carbon dioxide content of ant nests. This literature has been reviewed by Raignier (1948). Since Raignier's review two pa-

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[1] This is a portion of a dissertation submitted in partial fulfillment of the degree of Doctor of Philosophy in Zoology at the University of Chicago.

It is a pleasure to acknowledge the assistance given by many individuals. Dr. Alfred E. Emerson has been generous with his advice and criticism. Professors Thomas Park, Charles Olmsted and Paul Voth, all of the University of Chicago, were kind enough to supply suggestions and equipment on particular methodological problems.

My wife, Coral, has assisted in many aspects of the work, including the preparation of the manuscript.

pers on the microclimate in *Eciton* bivouacs have appeared, that of Schneirla *et al., loc. cit.* and that of Jackson (1957).

The moisture content of mound nests has received scant attention. Although he reported no measurements, Steiner (1929) felt that the mound moisture content must be lower than that of the soil, since xerophytes often grow on mound nest slopes. Stahel and Geijskes (1940) found the relative humidity within the subterranean fungus gardens of *Atta sexdens* to be between 91 percent and 97 percent. Raignier (1948), investigating day-night humidity changes in mound nests of *Formica rufa polyctena,* reported that relative humidity values fluctuated between 30 percent and 100 percent with humidity increasing with depth within the nest, and at night in the outer layers.

The present investigation was conducted at an aggregation of mound nests of *Formica ulkei* Emery located approximately 28 miles southwest of Chicago, near Lemont, Illinois. The study area consists of eighty acres of mixed oak-hickory forest situated on the Valparaiso terminal glacial moraine. The terrain is gently rolling upland dissected by sloping natural clearings and meadows. The clearings are poorly drained, swampy in part, and typically under water during spring and early summer. The soil is a heavy clay of glacial origin overlaid by a humus layer of varying thickness.

Almost uniformly the mound nests are located along the forest margin or at clearings in the forest, rarely within the forest (Dreyer and Park, 1932). The nest shape varies from conical with a circular base and narrow apex, to oblong with the longest basal diameter one to two times the width and with a rounded apex. Nests vary in height up to one meter, while the longest basal diameter observed is in excess of three meters. A typical large-sized mound is about 0.5 meters high and has a basal diameter of approximately 1.25 meters. The mounds are asymmetrical with a long broad slope facing toward the southwest, the direction of greatest solar radiation. If the southwest exposure is shaded by trees, then the long slope direction is shifted accordingly.

A cross section of the mound indicates that the nest is composed of a compact, laminated outer covering, up to two inches in thickness, over the porous nest interior. The interior portion of the mound consists of soil and decomposed vegetative debris. There are circular horizontal galleries as well as vertical galleries which extend as far as two meters into the subsoil. The surface is overlaid by a light covering of thatch, consisting of small twigs, grass stems, leaf petioles and leaf fragments.

The seasonal cycle of activity in *Formica ulkei* begins with the onset of higher air and nest temperatures in March or April. The adults, which survive the winter in the warmer subsoil beneath the mound, migrate upward and gradually commence nest construction and repair, and foraging. Eggs are laid in April and May, and development to the imago is completed in a single season. A mating flight takes place in July with queens returning to established nests. New nests are

formed by budding from certain of the active nests. In late September and October, as temperatures decline, activity gradually ceases as the adults migrate downward within the mound (Holmquist, 1928a and 1928b; Scherba, 1958).

REGULATION OF MOISTURE

MATERIALS AND METHODS

A suitable basis for assessing the extent to which the mound moisture content is regulated is to compare mound moisture values with those of the adjacent undisturbed and unmodified soil. To that end, samples of nest material and soil were collected from depths of 4 to 6 cm and 29 to 31 cm at 5 nests and from the soil adjacent to each of these nests at the same depths. Samples were collected at weekly intervals from May 5, 1953 to December 9, 1953, and from March 10, 1954 to April 30, 1954, at 9:30 to 11:30 a.m. C.S.T. The depths of 5 cm and 30 cm were selected after preliminary investigation indicated that moisture values at these depths were characteristic of those at the surface layer and mound interior, respectively.

Samples of approximately 50 grams were collected with the aid of hollow brass tubes, of 6 cm inside diameter, and a soil auger and sleeve, and were placed into air-tight numbered soil cans. Upon return to the laboratory the samples were weighed to the nearest 0.01 gram, oven-dried at 105°C. for 48 hours and reweighed. Moisture content is expressed as a percentage of oven-dry weight.

RESULTS

The moisture content of mound nests varies seasonally, being higher during the colder months and lower during the warmer season. Although obviously dependent upon precipitation, the seasonal pattern of rainfall and of nest moisture differ, indicating the action of other factors such as temperature upon nest moisture content (Fig. 1). For the 10-month period of measurement, the grand mean weekly moisture content, measured once per week, was 27.23 ± 0.66 percent at 5 cm and 29.40 ± 0.54 percent at 30 cm (Table I and Fig. 1). The range of mean weekly moisture values extended from 15.3 percent to 40.5 percent at 5 cm and from 21.6 percent to 40.7 percent at 30 cm.

During the colder months, the mean moisture content at 5 cm is higher than that at 30 cm, while the reverse holds true during the

TABLE I.—Grand mean weekly moisture content of 5 nests and adjacent soil, measured once per week May 5 to December 9, 1953 and March 10 to April 30, 1954

	5 cm. Mean ± S. E.	30 cm. Mean ± S. E.
Nest	27.23 ± 0.66%	29.40 ± 0.54%
Soil	38.54 ± 0.77%	23.89 ± 0.43%

active season. The vernal moisture inversion occurred during the middle of April in 1954 and the autumnal inversion during the middle of October in 1953 (Fig. 1).

There is a small vertical gradient of moisture present within the mounds between 5 cm and 30 cm depth. For the period of observation, the grand mean weekly moisture gradient was 5.40 ± 1.13 percent, and moisture gradient values, averaged for each month, varied from 3.0 percent to 6.0 percent. The range of this vertical moisture gradient varies seasonally and is higher during the colder months due to the increased moisture content at the 5 cm level (Fig. 2).

The moisture content of this series of mound nests differed from that of the adjacent soil in the following ways:

1. During the active season, the moisture content of the mound increases with depth, while in the soil the moisture content at 5 cm is consistently higher than that at 30 cm and does not show a seasonal inversion in the depth-moisture relationship (Figs. 1 and 3).

2. At the 5 cm level, the mean weekly moisture content of the soil, measured once per week, is significantly higher than that of the nest, while at the 30 cm depth, the nest moisture content is significantly higher than that of the soil (Figs. 1 and 3). These differences between means of nest and soil at the same depth are significant at the .01 or .001 level for each month with the exception of August at 30 cm and December at 5 cm and 30 cm.

3. The range of moisture values encountered at each particular depth decreases in this order; soil 5 cm, nest 5 cm, nest 30 cm, and soil 30 cm. Within the soil, the over-all range of mean weekly moisture values observed was 39.0 percent, while that for the nest during the same period of time, was 25.4 percent.

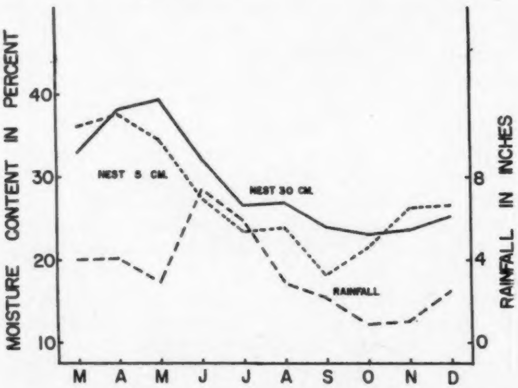

Fig. 1.—Seasonal cycle of mean weekly moisture content of 5 mound nests, May 5 to December 9, 1953 and March 10 to April 30, 1954, measured once each week.

4. The mean weekly vertical gradient of moisture present in the soil, 19.99 ± 1.48 percent is significantly greater than that in the nest, 5.40 ± 1.13 percent. This difference between nest and soil moisture gradients varies seasonally; it is greatest during March, April and May, and smallest during September and October.

5. Mound nests have a striking ability to withstand drought. An opportunity to observe this was presented from August 13 to September 3, 1953, when a 22-day drought occurred in the Chicago region. Maximum air temperatures were raised in excess of 90°F. for ten consecutive days and crop damage was severe. Weekly moisture observations during this period indicated that both nests and soil at a depth of 5 cm lost approximately 34 percent of their moisture content in three weeks. However, at a depth of 30 cm, the soil lost 29 percent of its moisture while the mound nests lost only 10 percent.

We may state that the moisture content of the measured portions of the mound environment is regulated by virtue of a higher, more uniform level of moisture, which varies over a smaller range of values than the adjacent unmodified soil at comparable depths.

MOISTURE PREFERENDUM

Since field measurements clearly show a modification of the mound moisture content as compared to that of the soil, we may inquire as to whether the moisture values encountered in the field represent an optimal level for this species, to the extent that this is indicated by laboratory preferendum tests in a gradient of soil moisture.

MATERIALS AND METHODS

Larvae, pupae and adults together with their nest material were collected in the field from an active nest, brought to the laboratory,

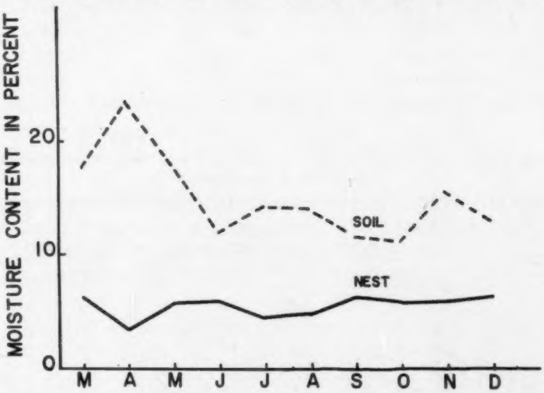

Fig. 2.—Seasonal cycle of mean weekly vertical gradient of moisture found between 5 cm and 30 cm depth in nest and soil, measured once each week.

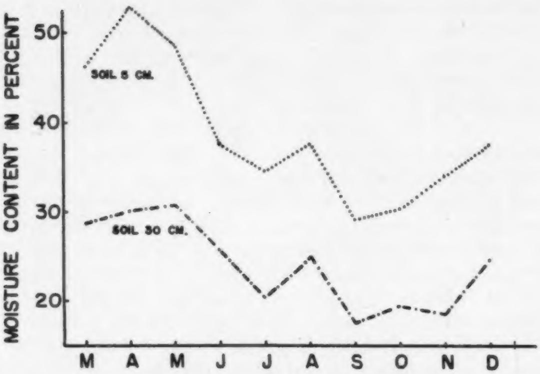

Fig. 3.—Seasonal cycle of mean weekly moisture content of soil adjacent to mound nests, May 5 to December 9, 1953 and March 10 to April 30, 1954, measured once each week.

and stored in gallon crocks in a refrigerator until needed.

The apparatus in which a gradient of soil moisture was established consisted of a metal, linear humidity gradient apparatus containing seven interconnecting chambers closed on three sides. The top of the apparatus was sealed with a plate glass cover. The apparatus, described by Emerson (1956), is 2½ cm high with each square chamber approximately 9 cm in diameter.

In establishing the gradient within the apparatus, nest material was sifted to eliminate particles larger than 2 mm and smaller than 0.5 mm in diameter, oven-dried at 110°C., cooled to room temperature and weighed into 100 gram batches. The appropriate amount of distilled water was then added to each batch in order to establish a gradient of soil moisture values, 0, 10, 20, 30, 35, 40, and 50 percent, arranged linearly in that order in the separate chambers of the

TABLE II.—Total number of live ants at each soil moisture chamber (all trials combined)

Percent Soil Moisture	Larvae		Pupae		Adults		Total	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final
0	28	0	54	3	49	3	131	6
10	28	0	54	8	49	7	131	15
20	28	43	54	133	49	36	131	212
30	28	56	54	78	49	68	131	202
35	28	70	54	121	49	70	131	261
40	28	1	54	1	49	24	131	26
50	28	0	54	1	49	12	131	13
TOTAL	196	170	378	345	343	220	917	739

apparatus. An equal number of larvae, pupae, and adults were then placed in each chamber, the glass cover was sealed with vaseline and the entire gradient was placed in a constant temperature room at 20°C. without light. The number of larvae, pupae and workers in each chamber was counted after 48 hours, and the soil in each chamber was weighed, dried and reweighed to detect any change in moisture content.

Four trials were run following a preliminary series. After 48 hours the soil in each chamber had lost approximately 2 percent soil moisture, except that in the 0 chamber which gained by that amount. Water droplets on the plate glass cover indicated that the air was saturated above chambers 20, 30, 35, 40 and 50.

RESULTS

From an original distribution of the brood and the adults in each chamber, the adults moved the immotile brood in such a way that the bulk of the population, 91.3 percent, was found in chambers 20, 30, and 35 (Table II). The differences between the total number of ants found at each of these three moisture levels are not significant.

The mean soil moisture preferendum differs for larvae, pupae and adults; it is higher for larvae than pupae, as might be expected. However, the differences between these three means are not significant (Table III). It is interesting to compare the mean moisture preferenda for pupae and larvae with the 10-month grand mean weekly mound moisture value as measured in the field. The agreement is striking (Table I, III).

Mortality in the apparatus was high, particularly for the adults. Mortality was more than three times higher in chamber 0 than in any of the other chambers, indicating that it is possible for workers to become "trapped" in unfavorable environments.

DISCUSSION

Evidently, one effect of mound nest construction is to produce a microclimate in which the moisture content is regulated in contrast to the adjacent soil at comparable depths. How is this regulation achieved?

There are no data which bear directly on this question. Nevertheless, it is possible to reach tentative conclusions on the basis of certain obvious physical relationships. The structure of the mound appears to be of prime importance. The thick crustal layer enclosing

TABLE III.—Mean soil moisture preferenda of *Formica ulkei*

	Mean ± S. E.	S. D.
Larvae	29.58 ± .039	.509
Pupae	27.58 ± .041	.764
Adults	21.07 ± .166	2.462

the mound and the high organic content of the nest material act to retain moisture and prevent excess water loss. High moisture levels are limited by the porosity of the mound interior and by the outer layer. The thatch covering atop the mound appears to impede erosion by raindrops. In addition, a certain degree of regulation probably results from the regular opening and closing of the nest entrances. Other, larger, crater-like openings are formed on the surface of *Formica rufa* mounds following rains, and Wellenstein (1928) suggests that these openings serve to decrease mound moisture. Similar openings are also found on *Formica ulkei* mounds, especially in the wet spring.

Several equally plausible explanations would explain the coincidence occurring between the grand mean weekly mound moisture levels and the mean soil moisture preferenda expressed by workers for larvae and pupae in a laboratory moisture gradient. Certainly the results are consistent with, but do not confirm, the hypothesis that the mound moisture level is regulated so as to approach an optimal level for development of the brood. Deviations from the preferendum level which must occur in different parts of the mound at different times in the day-night cycle and at different seasons, could be accommodated for by shifting the brood to a region in which there is a higher or lower level of moisture within the mound. Wheeler (1910) has suggested that such brood shifting does, in fact, occur.

The ability of an animal society to regulate a portion of its environment so as to decrease fluctuations about an optimal level, has been termed social homeostasis by Emerson (1954 and 1956), who reviews the history of this concept. In *Formica ulkei* mounds, the regulation of the mound moisture involves decreasing maximum levels, increasing minimum levels and decreasing the range of moisture fluctuation over that which is found in the adjacent unmodified soil at comparable depths. This regulation provides a specific example of a social homeostatic mechanism. Where this regulation is insufficient to provide optimum moisture levels, the ability of the workers to demonstrate a preferendum for the brood, and to shift the brood within the mound as the moisture level changes provides an elaboration of this mechanism.

SUMMARY

The moisture content of a series of five nests was compared with that of the adjacent soil at comparable depths, 5 cm and 30 cm, at weekly intervals over a period of ten months in order to determine if, as a result of mound nest construction, *Formica ulkei* regulates the moisture content of its environment.

Measurements indicated that the grand mean weekly moisture content of the mound, measured once per week, was 27.23 ± 0.66 percent at 5 cm and 29.40 ± 0.54 percent at 30 cm. A small gradient of moisture values exists between these depths, varying seasonally, with

a 10-month mean of 5.40 ± 1.13 percent. Observed fluctuations in the mean weekly moisture content ranged from 15.3 percent to 40.5 percent at 5 cm and from 21.6 percent to 40.7 percent at 30 cm.

It is concluded that these values indicate a regulated moisture content since, in contrast to the adjacent soil, mound nests have significantly higher minimum values at 30 cm, significantly lower maximum values at 5 cm and a significantly smaller gradient of moisture values existing between these depths. Also, the range of moisture values measured during the period of observation was smaller in the nests than in the soil.

Laboratory moisture gradient experiments indicate that workers are not indifferent to the moisture content of the environment and will shift larvae and pupae within a gradient of 0 to 50 percent soil moisture. The mean moisture preferenda for larvae, 29.58 ± 0.04 percent, and pupae, 27.58 ± 0.04 percent, coincide closely with the grand mean weekly moisture content of this series of mound nests.

Possible mechanisms of moisture regulation are suggested. The regulated moisture content of the mound environment, and the shifting of the brood by workers within a moisture gradient are interpreted as exemplifying the operation of a social homeostatic mechanism.

REFERENCES

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT 1949—Principles of Animal Ecology. Saunders, Philadelphia. 837 pp.

DREYER, W. A. AND T. PARK 1932—Local distribution of *Formica ulkei* mound nests with reference to certain ecological factors. Psyche **39** : 127-133.

EMERSON, A. E. 1954—Dynamic homeostasis: a unifying principle in organic, social and ethical evolution. Scient. Month. **78**: 67-75.

———1956—Regenerative behavior and social homeostasis in termites. Ecology **37**: 248-258.

FIRTH, H. J. 1956—Temperature regulation of the mallee-fowl, *Leiopoa ocellata* Gould. CSIRO Wildlife Res. **1** (2): 79-95.

HOLDAWAY, F. G. AND F. J. GAY 1948—Temperature studies of the habitat of *Eutermes exitosus* with special reference to the temperatures within the mound. Aust. J. Sci. Res. **1** (4): 464-493.

HOLMQUIST, A. M. 1928a—Notes on the life history and habits of the mound building ant *Formica ulkei* Emery. Ecology **9**:70-87.

———1928b—Studies in arthropod hibernation II. The hibernation of the ant, *Formica ulkei* Emery. Physiol. Zool. **1**:325-357.

JACKSON, W. B. 1957—Microclimate patterns in the army ant bivouac. Ecology **38**:276-285.

LEWIS, F. 1940—Notes on the breeding habits of the mallee-fowl. Emu **40**:97-110.

RAIGNIER, A. 1948—L'economie thermique d'une colonie polycalique de la fourmi des bois. Cellule **51**:279-368.

SCHERBA, G. 1958—Nest orientation, reproduction and population structure of an aggregation of mound nests of *Formica ulkei* Emery. Insectes Soc. **5**:201-213.

SCHNEIRLA, T. C., R. C. BROWN AND F. C. BROWN 1954—The bivouac or temporary nest as an adaptive factor in certain terrestrial species of army ants. Ecol. Monogr. **24**:269-296.

STAHEL, G. AND D. GEIJSKES 1940—Observations about temperature and moisture in *Atta* nests. Rev. de Ent. **11**:766-775.

STEINER, A. 1929—Temperaturuntersuchungen in Ameisennestern mit Erdkuppen, im Nest von *Formica exsecta* Nyl. und in Nestern unter steinen. Zeit. vergl. Physiol. **9**:1-66.

WELLENSTEIN, G. 1928—Beitrage zur Biologie der roten Waldameise (*Formica rufa* L.) mit besonderer Berüksichtigung Klimatischer und forsticher Verhältnisse. Zeit. Ang. Ent. **14**:1-68.

WHEELER, W. M. 1910—Ants. Columbia U. Press, New York, 663 pp.

Notes and Discussions

Occurrence of Nipplewort in Indiana

Although both Fernald, in the 8th edition of *Gray's Manual,* and Gleason, in the *New Britton and Brown Illustrated Flora,* refer to the Eurasian composite *Lapsana communis* L. as widely established in North America from Quebec and Ontario south to Virginia and Missouri (in the West to Colorado and California), it has not been reported heretofore from Indiana either in Deam's *Flora* (1940) or in the several *Indiana Plant Distribution Rec*ords (1940-1950) supplementing that work. On June 2, 1958, the writer noted an extensive colony of nipplewort, some 250 to 300 plants, in an area about 35 by 20 feet on the north side of the road at the northwest corner of the laundry, University of Notre Dame. Specimens have been deposited in the U. S. National Herbarium (where the nearest locality in the representation of this species is Oakland County, Michigan) and in the writer's herbarium.—P. E. HEBERT, C.S.C., Notre Dame, Indiana.

Phyllopod Shrimp Populations of the Big Alkali Lake Drainage, Nebraska and Their Relationship to Young Pike (Esox lucius)[1]

Random sampling with a fine-mesh dip net in the drainage pools south of Big Alkali Lake, Cherry County, Nebraska, indicated a spring abundance of anostracan and notostracan phyllopods, commonly called fairy shrimps and tadpole shrimps. Collections were made during the months of April and May of 1957 and 1958, and specimens were submitted to Dr. Ralph W. Dexter, Professor of Biology, Kent State University, Ohio, for identification. The 1957 collections were fairy shrimps of the species *Chirocephalopsis bundyi* while those of 1958 were tadpole shrimps, *Lepidurus couesi.* The presence of *L. couesi* establishes a new state record for this phyllopod.

Since the occurrence of these shrimps appeared widespread throughout the Big Alkali drainage, we were interested in the utilization of this type of forage by northern pike fingerlings.

The prairie pools from which the shrimps were collected fill with water each spring and are normally dry by late summer. However, several of the larger pools, five to eight acres in size, retain some water during normal years of rainfall. Periodic pool fluctuations result from cyclic occurrence of excessive or deficient precipitation in association with poor drainage. The vegetation consists primarily of sedges and hydrophytic grasses, with halophytes present in saline areas.

Approximately 60 percent of the drainage pools sampled contained fairy shrimps or tadpole shrimps with both types of phyllopods common in pools connected by flowing water. Undoubtedly, many shrimps are washed downstream into Big Alkali Lake proper where they furnish available forage for the lake's fish population. Dip net sampling of the lake shoreline, some distance from the drainage ditch entrance, failed to reveal presence of a resident lake shrimp population.

Adult spawning pike enter the inlet drainage ditch around the third week in March. Spawning activity takes place throughout the entire three square miles of drainage and often in pools associated with shrimp populations. Spot

rotenone sampling in late April and early May revealed the co-habitation of 2.5 - 3.5 inch pike fingerlings with shrimps in many of the pools. Stomach contents from 16 young pike showed a 100 percent occurrence of shrimps. The average length of these fingerlings (3.1 inches), compared to specimens collected in habitat where phyllopod shrimp did not occur, was about 1.0 inches larger. Such meagre evidence to date does point to an accelerated growth of pike fingerlings found in phyllopod shrimp pools. The sporadic and ephemeral nature of the occurrence of these shrimps tends to preclude any forecast of specific pool abundance until field checks are conducted each spring. The movement of young pike into shrimp pools for feeding is not conclusive but this possibility does exist.

In the field of fisheries management, the ecological relationship between the seasonal abundance of phyllopod shrimps and growth of fingerling pike should be of value in the classification of pike habitat.—D. BRUCE MCCARRAHER, District Fisheries Supervisor, Bassett, Nebraska.

[1] A contribution from Federal Aid project F-4-R, Job No. 2, Sandhill Lakes Survey. Nebraska Game, Forestation and Parks Commission.

Supplement to "Flora of Saskatchewan"

The following additions and corrections will bring up to date my *Annotated Catalogue of the Vascular Flora of Saskatchewan,* published in the *American Midland Naturalist* **58**:1-72, 1957.

Page 5.—For *Botrychium matricariifolium* substitute: *B. matricariifolium* R. Br. (*B. lanceolatum* and *B. simplex* of Sask. reports, nor Ångstr. nor E. Hitchc.).—Chamomile-leaved Grape-fern. Cypress Hills (UNS); Mortlach (DAS, DAO); Amisk Lake (DAS, DAO). Ssp. *hesperium* Maxon & Clausen (var. *hesperium* (Maxon & Clausen) Boivin). Beechy (DAS, DAO). Determined by R. T. Clausen.

Page 6.—For *Isoëtes muricata* substitute: *Isoëtes echinospora* Durieu var. *braunii* (Durieu) Engelm. (*I. muricata* Durieu var. *braunii* (Durieu) Reed.

Page 10.—Between *Bromus tectorum* and *Calamagrostis canadensis* insert: *Buchloe dactyloides* (Nutt.) Engelm. Buffalo-grass. Estevan, J. H. Hudson, Aug. 4, 1957, No. 1996 (DAS, DAO).

Page 12.—Between lines 7 and 8 from top, insert: *Eragrostis hymenoides* (Lam.) BSP. Creeping Love Grass. Glen Ewen, J. H. Hudson, Sept. 5, 1957, No. 2017 (DAS, DAO).

Page 13.—For "Brunyee's Ranch near Verlo, about 50° 22′N., 108° 39′ W." after *Munroa squarrosa* substitute: Brunyee's Ranch in Valley of the South Saskatchewan River near Saskatchewan Landing.

Page 14.—Delete *Poa nervosa.* Specimens assigned to this species should be transferred to *Poa secunda.*

Page 16.—Between line 5 and 6 from top, insert: *Carex granularis* Muhl. var. *haleana* (Olney) Porter. Granular Sedge. Moist meadow. Spy Hill, J. H. Hudson, June 18, 1958, No. 2049 (DAO).

Page 16.—Between line 5 and 6 from top insert: *Carex gravida* Bailey. Heavy-fruited Sedge. Roche Percée, J. H. Hudson, Aug. 4, 1957, No. 1999 (DAS, DAO). Alphabetically, this entity follows *C. granularis* var. *haleana.*

Page 17.—Following *Carex stenophylla* Wahl. ssp. *elecharis* (Bailey) Hultén, add the synonym: *C. stenophylla* var. *enervis* (C. A. Mey.) *Kükenth* for those who prefer to use the varietal category.

Page 18.—Under *Eleocharis compressa,* the specimens cited from McKague

217, Wallwort 1380 and Nipawin 6030 proved to be *Eleocharis elliptica* Knuth.

Page 19.—Between *Scirpus americanus* and *Scirpus caespitosus* var. *callosus* insert: *Scirpus atrovirens* Willd. var. *pallidus* Britt. Dark-green Bulrush. Glen Ewen, J. H. Hudson, Sept. 15, 1957, No. 2021 (DAS, DAO).

Page 19.—For *Scirpus microcarpus* substitute: *Scirpus microcarpus* Presl. var. *rubrotinctus* (Fern.) M. E. Jones. Bull. Univ. Montana Biol. Ser. 15: 20, 1910.

Page 21.—*Streptopus amplexifolius* substitute: *Streptopus amplexifolius* (L.) DC. var. *americanus* Schultes.

Page 24.—To *Salix mackenzieana* add the locality: Beauval along the Beaver River 140 miles NE of Meadow Lake (DAO).

Page 25.—For *Salix phyllicifolia* read: *S. phylicifolia.*

Page 26.—For *Laportea canadensis* (L.) Gaud. substitute: *Laportea canadensis* (L.) Wedd.

Page 28.—Following *Chenopodium pratericola* Rydb. ssp. *desiccatum* add the synonym: *C. pratericola* var. *oblongifolium* (S. Wats.) Wahl., for those who prefer to use the varietal category.

Page 29.—For *Cyclocoma* read: *Cycloloma.*

Page 32.—For *Myosurus minimus* ssp. *montananus* substitute: *M. aristatus* Benth. ex Hook. ssp. *montanus* (Campbell) Stone in Mason, Flora of California Marshes, 503, 1957.

Page 34.—Between *Camelina sativa* and *Cardamine pensylvanica* insert: *Capsella bursa-pastorus* (L.) Medic. Shepherd's Purse. Common introduced weed in fields and waste places. This species was inadvertently omitted from the Catalogue.

Page 35.—Between lines 21 and 22 from top, insert: *Draba reptans* (Lam.) Fern. var. *micrantha* (Nutt.) Fern. Gravel pit along Roughbark Creek south of Hallerite, J. H. Hudson in 1958 (DAO).

Page 35.—For *Draba nemoralis* read: *Draba nemorosa.*

Page 36.—For *Pteritoma* read: *Peritoma.*

Page 36.—For *Polanesia* read: *Polanisia.*

Page 38.—Delete *Crataegus columbiana* Howell. Specimens assigned to this species should be transferred to *Crataegus chrysocarpa* Ashe. This correction should also be made in Can. Field-Nat. 68: 82, 1954 and 71: 57, 1957.

Page 39.—For *Potentilla pectinata* substitute: *Potentilla pensylvanica* var. *pectinata* (Raf.) Lepage.

Page 41.—Between lines 20 and 21 from top, insert: *Astragalus purshi* Dougl. ex Hook. Pursh's Milk Vetch. Short grass prairie. Climax, G. F. Ledingham and J. H. Hudson, May 18, 1958, No. 2022 (DAO). Previous reports of *A. purshii* from Sask., proved to be the similar *A. lotiflorus.*

Page 42.—Between lines 23 and 24 from the bottom insert: *Petalostemon villosum* Nutt. Hairy Prairie Clover. Bottom of sand blowouts. Mortlach, J. H. Hudson, Aug. 15, 1955, No. 1735 (DAS, DAO).

Page 44.—Between ANACARDIACEAE and ACERACEAE insert: CELASTRACEAE *Celastrus scandens* L. Climbing Bittersweet. Estevan, J. H. Hudson, Aug. 3, 1957, No. 1993 (DAS, DAO).

Page 44.—For *Malva neglecta* substitute: *Malva rotundifolia* L. Round-leaved Mallow.

Page 45.—For LOSACEAE read: LOASACEAE.

Page 47.—For *Cymopteris* read: *Cymopterus.*

Page 51.—Add *Asclepias verticillata* L. Whorled Milkweed. Estevan, J. H. Hudson, Aug. 4, 1957, No. 1998 (DAS, DAO).

Page 52.—Under *Cryptantha macounii*, the synonym *O. apera* should read: *O. aperta*.

Page 52.—For the colloquial name Hoary Poccoon of *Lithospermum canescens* substitute Hoary Puccoon.

Page 53.—*For Scutellaria galericulata* substitute: *Scutellaria galericulata* L. var. *epilobiifolia* (A. Hamilt.) Jordal.

Page 56.—For *Galium boreale* substitute: *Galium septentrionale* Roem. & Schult. (*G. boreale* of Amer. auth., not L.). See A. & D. Löve, Amer. Midl. Nat. 52: 88-105, 1954.

Page 59.—Between line 20 and 21 from top, insert: *Antennaria dimorpha* (Nutt.) Torrey & Gray. Short grass prairie. Climax, G. F. Ledingham & J. H. Hudson, May 18, 1958, No. 2023 (DAS, DAO); Divide, G. F. Ledingham & J. H. Hudson, May 19, 1958, No. 2025 (DAO).

Page 61.—Line 22 from bottom delete: *A. tweedyi*.

Page 61.—Between lines 18 and 19 from bottom, insert: *Aster hesperius* var. *laetevirens* (Greene) Cronq. (A. tweedyi of Fraser & Russell, not Rydb.) Swift Current, J. L. Bolton, Sept. 10, 1936, No. 155 (UNS). Determined by A. Cronquist.

Page 62.—Between lines 8 and 9 from top, insert: *Aster umbellatus* Mill. var. *pubens* A. Gray (*Doellingeria pubens* (A. Gray) Rydb.). Flat-topped Aster. Spy Hill, J. H. Hudson, Aug. 17, 1957, No. 2003 (DAS, DAO).

Page 62.—On line 9 from top, for *Picardeniopsis* read: *Picradeniopsis*.

Page 62.—On line 7 from bottom, for *Cirsium flodmanii* f. *albiflora* Löve, substitute: *C. flodmanii* f. *albiflora* D. Löve.

Page 63.—Lines 30 and 32 from bottom. For Lunnell read: Lunell.

Page 63.—Delete *Erigeron pumilus* Nutt. Specimens assigned to this species proved to be *Erigeron caespitosus* Nutt. Determinations by A. Cronquist.

Page 65.—Between lines 4 and 5 from top, insert: *Helianthus tuberosus* L. var. *subcanescens* A. Gray (*H. subcanescens* A. Gray). Jerusalem Artichoke. Northgate, J. H. Hudson, Sept. 8, 1957, No. 2016 (DAS, DAO).

Page 65.—Delete *Liatris aspera*. Specimens assigned to this species should be transferred to *Liatris ligulistylis*.

Page 66.—Lines 13 to 19 from top. Delete *Senecio pauperculus* var. *thompsoniensis* (Greene) Boivin. Dr. Cronquist examined a specimen cited as *Senecio pauperculus* var. *thompsoniensis*, Cypress Hills, A. J. Breitung, No. 4313, which he considers is more closely related to *Senecio pseudaureus*.

Page 68.—For *Microseris cuspidatum* read: *Microseris cuspidata*.—August J. Breitung, Glendale, California.

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Manuscripts should be typewritten, double-spaced, with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The title and author's name along with the full mailing address of the author should be placed on the first page.

Style, arrangement, spelling, and abbreviations should conform to the usage of recent numbers of this journal. Do not underline any words except scientific names. Acknowledgments can be included in the Introduction, or may be offered as a footnote attached to the title of the article.

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References should be listed alphabetically by authors' names. In the text they should be cited by author and date, e.g., Smith (1958). The form of the citations should be that used in this journal; in references to papers in periodicals, titles should be given and inclusive page numbers are required. All citations should be checked with the original articles. Abbreviations of the names of periodicals should conform with the listings in BIOLOGICAL ABSTRACTS 29(5):v-xxxv (May, 1955), or 30(5):xi-xxxii (May, 1956). Book citations should include author's name, complete title, edition, name and location of publisher, and total number of pages.

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